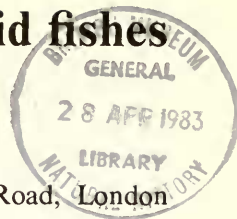


# The *Ophthalmotilapia* assemblage of cichlid fishes reconsidered

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## Synopsis

The *Ophthalmotilapia* assemblage of cichlid fishes from Lake Tanganyika, first defined by Liem (1981), originally comprised the genera *Asprotilapia*, *Ectodus*, *Lestradea*, *Cunningtonia* and *Ophthalmotilapia* (with which was synonymized *Ophthalmochromis*). The characters on which the assemblage was based are reviewed and revised in the light of information derived from large-scale outgroup comparisons.

As a result of this review, five additional genera can be included in the assemblage (viz. *Aulonocranus*, *Grammatotria*, *Callochromis*, *Xenotilapia* and *Cyathopharynx* (with which *Cardiopharynx* is synonymized). Two lineages within the *Ophthalmotilapia* assemblage are defined.

Previous schemes of supposed relationships for these taxa are discussed, as is the problem of identifying the sister-group for the assemblage. No sister-group can be identified amongst the endemic taxa of Lake Tanganyika, but the possibility of an endemic taxon from Lake Malawi being the sister-group is explored.

Problems arising from possible homoplasy and thus the misidentification of sister-groups are illustrated by examples involving cichlid species from Lakes Tanganyika and Malawi, and from these lakes and Lake Fwa (Zaire drainage basin).

## Introduction

During the last thirty years there has been a marked increase in our knowledge of taxonomic and ecological diversity amongst African cichlid fishes. Unfortunately there has been less progress made in our understanding of phyletic relationships between the various elements of those faunas, or even amongst members of the so-called species flocks of the major African lakes (see Greenwood, 1980).

Two recent papers are welcome and important contributions to the field of phyletic studies since both are concerned with interrelationships in a single species flock, that of Lake Tanganyika (Liem & Stewart, 1976; Liem, 1981).

Liem's (1981) paper is directed at establishing the monophyletic origin of five endemic genera from that lake, viz. *Asprotilapia*, *Ectodus*, *Lestradea*, *Cunningtonia* and *Ophthalmotilapia*. Although Liem was able to argue a case for recognizing the monophyly of these taxa (the *Ophthalmotilapia* assemblage), and the intragroup relationships of its constituent genera, he was unable to recognize a sister-group for the whole assemblage. He did, however, suggest that among the endemic Tanganyika genera, *Aulonocranus*, *Xenotilapia*, *Callochromis* and *Cardiopharynx* share some of the derived features characterizing the *Ophthalmotilapia* assemblage (Liem, 1981 : 206; 208).

My interest in these species, and the *Ophthalmotilapia* lineage, stems from my current research into the levels of relationship existing between the endemic cichlid genera of Lakes Victoria, Malawi and Tanganyika (Greenwood, 1979; 1980). Using information acquired in this search, it seemed that Liem's concept of the *Ophthalmotilapia* assemblage could be extended to include several other Tanganyika taxa, including those suspected of such relationship by Liem. It was also apparent that the group characters for the assemblage should be reviewed in the light of more extensive outgroup comparisons than were employed originally.

Finally, my interest was aroused by what seemed to be the unusually clear light that some members of the *Ophthalmotilapia* assemblage could throw on the longstanding and often intractable problem of homoplasy and its effects on hypotheses of relationship amongst African cichlid fishes.

Like Liem, I have been unable to identify a sister-group for the *Ophthalmotilapia* assemblage from amongst the Tanganyika cichlids. A very tentative suggestion can be made, however, for a possible sister-group relationship between the assemblage and certain members of the Lake Malawi flock.

### Material examined

Dissections were made of the dorsal gill-arch musculature in one, or usually 2, specimens of each genus now included in the *Ophthalmotilapia* assemblage (see p. 278). The specimen of *Asprotilapia leptura* (BMNH 1906.9.6 : 157) was that used by Liem (1981) but the jaw muscles of the left side were freshly dissected.

The nature of the gut and its coiling pattern were checked in several specimens of each *Ophthalmotilapia* assemblage species (except *Asprotilapia leptura* where only the type and the specimen noted above could be used).

Jaw and dorsal gill-arch muscles were dissected in unregistered specimens of *Astatotilapia elegans* and in *A. burtoni*.

All available dry skeletal material in the BM(NH) collections was examined, in particular that prepared for the revisions of the Lake Victoria, Edward-George, Kivu, and Turkana haplochromine species (see Greenwood, 1980). Additional material, prepared for this paper, and alizarin transparencies not previously listed, are given below. The taxa are first grouped geographically, and then alphabetically, within the categories: Dry skeleton (DS) and Alizarin transparency (AT).

#### Lake Tanganyika

##### DS:

<i>Asprotilapia leptura</i>	671
<i>Aulonocranus dewindti</i>	1960.9.30 : 4629-641
<i>Callochromis macrops</i>	1906.9.8 : 178
<i>Cardiopharynx schoutedeni</i>	1950.4.1. : 1854-81; 1960.9.30 : 1647-56
<i>Cyathopharynx furcifer</i>	1900.9.8 : 251; 148; 1950.4.1 : 1714-47

<i>Cunningtonia longiventralis</i>	1950.4.1 : 1265–1281
<i>Ectodus descampsi</i>	1906.9.8 : 194; 1950.4.1 : 3066–67
<i>Eretmodus cyanostictus</i>	1950.4.1 : 5171–82; 693
<i>Grammatotria lemairei</i>	1950.4.1 : 3758–3785
<i>Lestradea perspicax stappersi</i>	1960.9.30 : 1553–1557
<i>Limnochromis auritus</i>	1906.9.6 : 71
<i>Limnochromis leptosoma</i>	1906.9.6 : 83
<i>Lobochilotes labiatus</i>	1950.4.1 : 554–566; 567–579; 590–606
<i>Neotilapia tanganyicae</i>	1900.12.13 : 35
<i>Ophthalmotilapia boops</i>	1960.9.30 : 1720–1724
<i>Ophthalmotilapia ventralis</i>	1906.9.8 : 144
<i>Perissodus microlepis</i>	Uncatalogued
<i>Perissodus paradoxus</i>	1906.9.8 : 267
<i>Petrochromis famula</i>	1950.4.1 : 7642–52
<i>Petrochromis fasciolatus</i>	1960.9.30 : 1368–71; 1372–75
<i>Petrochromis polyodon</i>	1898.9.9 : 66; 1950.4.1 : 7608–611; uncatalogued
<i>Simochromis babaulti</i>	Uncatalogued
<i>Simochromis curvifrons</i>	1955.4.12 : 47–66; uncatalogued
<i>Simochromis dardennei</i>	1906.9.8 : 244; uncatalogued (4 specimens)
<i>Simochromis diagramma</i>	1906.9.8 : 217; uncatalogued
<i>Simochromis loocki</i>	1950.4.1 : 7674–7701; 7702–7728
<i>Trematocara marginatum</i>	1960.9.30 : 4835–4850
<i>Trematocara unimaculatum</i>	1906.9.6 : 119
<i>Tropheus moorei</i>	1950.4.1 : 907–67; uncatalogued
<i>Xenotilapia boulengeri</i>	1961.11.22 : 290–293

## AT:

<i>Astatotilapia burtoni</i>	1960.9.30 : 2415–33
<i>Aulonocranus dewindti</i>	1950.4.1 : 4695–775; 4642–656
<i>Callochromis macrops macrops</i>	1960.9.20 : 2821–2823
<i>Callochromis macrops melanostigma</i>	1960.9.30 : 2845–2859
<i>Cardiopharynx schoutedeni</i>	1960.9.30 : 1574–1615
<i>Ctenochromis horei</i>	1960.9.30 : 2526–28
<i>Cunningtonia longiventralis</i>	1960.9.30 : 1896–1907
<i>Cyathopharynx furcifer</i>	1960.9.30 : 1792–1802
<i>Ectodus descampsi</i>	1961.11.22 : 113–119
<i>Eretmodus cyanostictus</i>	1950.4.1 : 5171–5182
<i>Grammatotria lemairei</i>	1960.9.30 : 3317–30; 3276–79; 3208–21
<i>Hemibates stenosoma</i>	1961.11.22 : 976–989
<i>Lamprologus brevis</i>	1960.9.30 : 7181–7225
<i>Lamprologus cunningtoni</i>	1950.4.1 : 6701–6707
<i>Lamprologus elongatus</i>	1960.9.30 : 6851–6860
<i>Lamprologus fasciatus</i>	1950.4.1 : 7075
<i>Lamprologus tetracanthus</i>	1960.9.30 : 7309–7336
<i>Lamprologus werneri</i>	1976.5.21 : 46–65
<i>Lestradea perspicax</i>	1960.9.30 : 1468–84
<i>Limnochromis abeelei</i>	1961.11.22 : 56–58
<i>Limnochromis auritus</i>	1960.9.30 : 1981–85
<i>Limnochromis dhanisi</i>	1960.9.30 : 2001–04
<i>Limnochromis otostigma</i>	1960.9.30 : 1989–97
<i>Limnochromis pfefferi</i>	1960.9.30 : 1923–26
<i>Limnochromis permaxillaris</i>	1961.11.22 : 41–46
<i>Ophthalmotilapia boops</i>	1960.9.30 : 1716–18; 1720–24
<i>Ophthalmotilapia ventralis</i>	1960.9.30 : 1689–94
<i>Perissodus hecqui</i>	1960.9.30 : 6364–69
<i>Perissodus microlepis</i>	1960.9.30 : 6386–91
<i>Perissodus paradoxus</i>	1960.9.30 : 6468–6482
<i>Petrochromis fasciolatus</i>	1960.9.30 : 1392–93; 1394–96; 1390
<i>Petrochromis polyodon</i>	1960.9.30 : 1359–63

<i>Simochromis curvifrons</i>	1961.11.22 : 2-8
<i>Simochromis dardennei</i>	1960.9.30 : 1061
<i>Simochromis diagramma</i>	1960.9.30 : 1170-1174; 1188-91
<i>Simochromis loocki</i>	1950.4.1 : 7702-28
<i>Telmatochromis temporalis</i>	1960.9.30 : 6531-6538
<i>Trematocara caparti</i>	1961.11.22 : 703-721
<i>Trematocara kufferathi</i>	1961.11.22 : 883-910
<i>Trematocara marginatum</i>	1960.9.30 : 4881-90
<i>Trematocara nigrifrons</i>	1961.11.22 : 693-703; 1960.9.30 : 4990-5019
<i>Trematocara stigmaticum</i>	1960.9.30 : 5143-171
<i>Trematocara unimaculatum</i>	1961.11.22 : 519-528
<i>Tropheus moorei</i>	1961.11.22 : 13
<i>Xenotilapia boulengeri</i>	1961.11.22 : 225
<i>Xenotilapia melanogenys</i>	1950.4.1 : 4035-40; 1960.9.30 : 3449-455
<i>Xenotilapia ochrogenys</i>	1960.9.30 : 3820-855
<i>Xenotilapia sima</i>	1961.11.22 : 208-211
<i>Xenotilapia tenuidentata</i>	1960.9.30 : 7998-8014

### Lake Malawi

#### DS:

<i>Astatotilapia calliptera</i>	1893.11.15 : 4
<i>Aulonocara nyassae</i>	1935.6.14 : 2259-63; 681.5A
<i>Aulonocara rostrata</i>	681.5A
<i>Chilotilapia rhoadesii</i>	681.2; 1935.6.14 : 2103-211
<i>Corematodus shiranus</i>	681.4A
<i>Corematodus taeniatus</i>	681.4B; 681.4C
<i>Cyathochromis obliquidens</i>	1935.6.14 : 282-295; 681.12A : 681.12B
<i>Cynotilapia afra</i>	1893.1.17 : 8 (syntype)
<i>Docimodus johnstoni</i>	681.3
<i>Genyochromis mento</i>	1965.10.26 : 24-29
<i>Gephyrochromis lawsi</i>	1965.11.2 : 14-22 (paratypes)
' <i>Haplochromis</i> ' <i>ahli</i>	1935.6.14 : 1469-71
' <i>Haplochromis</i> ' <i>annectens</i>	1935.6.14 : 847-52
' <i>Haplochromis</i> ' <i>argyrosoma</i>	1935.6.14 : 1657-61
' <i>Haplochromis</i> ' <i>atrिताeniatus</i>	1935.6.14 : 1426-9
' <i>Haplochromis</i> ' <i>auromarginatus</i>	1935.6.14 : 1476-78
' <i>Haplochromis</i> ' <i>breviceps</i>	1935.6.14 : 870-72
' <i>Haplochromis</i> ' <i>caeruleus</i>	1935.6.14 : 1267-69
' <i>Haplochromis</i> ' <i>chrysonotus</i>	1935.6.14 : 1823-32
' <i>Haplochromis</i> ' <i>dimidiatus</i>	1935.6.14 : 1154-71
' <i>Haplochromis</i> ' <i>ericotaenia</i>	1935.6.14 : 2405-2411
' <i>Haplochromis</i> ' <i>euchilus</i>	1972.9.13 : 70
' <i>Haplochromis</i> ' <i>eucinostomus</i>	1962.10.18 : 1-10
' <i>Haplochromis</i> ' <i>fuscotaeniatus</i>	1935.6.14 : 494-95
' <i>Haplochromis</i> ' <i>guentheri</i>	1921.9.6 : 154-62
' <i>Haplochromis</i> ' <i>intermedius</i>	1972.9.13 : 91-94
' <i>Haplochromis</i> ' <i>johnstoni</i>	1935.6.14 : 523-32
' <i>Haplochromis</i> ' <i>kirkii</i>	1935.6.14 : 953-62
' <i>Haplochromis</i> ' <i>kiwinge</i>	1935.6.14 : 1031-40
' <i>Haplochromis</i> ' <i>labifer</i>	1972.9.13 : 77-81
' <i>Haplochromis</i> ' <i>labridens</i>	1935.6.14 : 991-1000; 1001-05
' <i>Haplochromis</i> ' <i>lateristriga</i>	1935.6.14 : 1209-18
' <i>Haplochromis</i> ' <i>lepturus</i>	1935.6.14 : 1340-56
' <i>Haplochromis</i> ' <i>longimanus</i>	1972.12.20 : 35-78
' <i>Haplochromis</i> ' <i>macrostoma</i>	1935.6.14 : 605-7
' <i>Haplochromis</i> ' <i>marginatus</i>	1935.6.14 : 769-77
' <i>Haplochromis</i> ' <i>moorii</i>	1935.6.14 : 1692-1700
' <i>Haplochromis</i> ' <i>nototaenia</i>	1935.6.14 : 1378-84
' <i>Haplochromis</i> ' <i>ornatus</i>	1972.12.18 : 31-33



<i>'Haplochromis' orthognathus</i>	1973.3.26 : 189; 1969.3.11 : 19
<i>'Haplochromis' placodon</i>	1935.6.14 : 1736–45
<i>'Haplochromis' pleurotaenia</i>	1935.6.14 : 911–16
<i>'Haplochromis' polystigma</i>	1935.6.14 : 433–37
<i>'Haplochromis' quadrimaculatus</i>	1935.6.14 : 1960–69
<i>'Haplochromis' prostoma</i>	1962.10.18 : 59–71; 1979.11.26 : 5–9
<i>'Haplochromis' rhoadesii</i>	681T
<i>'Haplochromis' rostratus</i>	1935.6.14 : 549–54
<i>'Haplochromis' semipalatus</i>	1956.6.12 : 9–10
<i>'Haplochromis' spilonotus</i>	1969.3.11 : 11–14
<i>'Haplochromis' spilorrhynchus</i>	1935.6.14 : 1260–4
<i>'Haplochromis' subocularis</i>	1935.6.14 : 1180–89
<i>'Haplochromis' tetrastigma</i>	1935.6.14 : 1556–66; 1567–77
<i>Hemitilapia oxyrhynchus</i>	1906.9.7 : 39
<i>Labeotropheus fuelleborni</i>	1972.8.11 : 3–5; 681.11
<i>Labidochromis vellicans</i>	1965.10.26 : 14–21
<i>Labidochromis zebroides</i>	1981.1.9 : 102–106 (paratype)
<i>Lethrinops auritus</i>	1930.1.31 : 84–86
<i>Lethrinops lethrinus</i>	1930.1.31 : 150–4; 1906.9.7 : 35
<i>Lethrinops longimanus</i>	1969.3.11 : 20–23
<i>Lethrinops parvidens</i>	1935.6.14 : 2070–73
<i>Lethrinops praeorbitalis</i>	696J
<i>Melanochromis melanopterus</i>	1935.6.14 : 303 (syntype); 1971.9.13 : 32–36
<i>Melanochromis vermivorous</i>	1935.6.14 : 307–16 (syntype)
<i>Petrotilapia tridentiger</i>	1981.2.2 : 212–20; 681.9
<i>Pseudotropheus fuscus</i>	1965.10.25 : 131–41
<i>Pseudotropheus livingstoni</i>	1935.6.14 : 128–30
<i>Pseudotropheus lucerna</i>	1935.6.14 : 165–9 (syntype)
<i>Pseudotropheus macrophthalmus</i>	Uncatalogued
<i>Pseudotropheus tropheops</i>	1965.10.25 : 115–24; 681.8C
<i>Pseudotropheus williamsi</i>	1965.10.25 : 20–26; 681.8B
<i>Pseudotropheus zebra</i>	1935.6.14 : 135–40; 681.8A
<i>Trematocranus microstoma</i>	1935.6.14 : 2232–6

## AT:

<i>Astatotilapia calliptera</i>	1966.7.26 : 17–42
<i>Aulonocara nyassae</i>	1935.6.14 : 2259–63
<i>Lethrinops lethrinus</i>	1930.1.31 : 109–118

## Elsewhere

## DS:

<i>Astatotilapia bloyeti</i>	1961.12.1 : 341–353
<i>Astatotilapia nubila</i>	1911.3.3 : 148
<i>Chromidotilapia batesii</i>	1912.6.29 : 4
<i>Chromidotilapia kingsleyae</i>	1912.4.1 : 526; 1908.5.30 : 186
<i>Oreochromis niloticus</i>	662D; Uncatalogued
<i>Tilapia rendalli</i>	1906.9.7 : 32
<i>Tilapia zilli</i>	1907.12.2 : 3767

## AT:

<i>Astatotilapia bloyeti</i>	Uncatalogued
<i>Astatotilapia macropsoides</i>	Uncatalogued
<i>Oreochromis niloticus</i>	1907.12.2 : 3533–534

Radiographs used in this study were:

## Lake Tanganyika

<i>Asprottilapia leptura</i>	1906.9.6 : 156–157 (FW 677)
<i>Aulonocranus dewindti</i>	1950.4.1 : 4843–93 (FW678)
<i>Callochromis macrops macrops</i>	1950.4.1 : 3258–312 (FW683)

<i>Callochromis macrops melanostigma</i>	1960.9.30 : 2882–96 (FW683)
<i>Callochromis pleurospilus</i>	1940.4.1 : 3458–662; 1920.5.25 : 152–53 (FW682)
<i>Cardiopharynx schoutedeni</i>	1960.9.30 : 1574–1615 (FW674)
<i>Cunningtonia longiventralis</i>	1950.4.1 : 1282–86 (FW676)
<i>Cyathopharynx furcifer</i>	1950.4.1 : 1605–37; 1906.9.8 : 249–251 (FW673)
<i>Ectodus descampsi</i>	1961.11.22 : 76–87 (FW677)
<i>Grammatotria lemairei</i>	1950.4.1 : 3703–3727 (FW684)
<i>Lestradea perspicax</i>	1950.4.1 : 1531–46 (FW676)
<i>Ophthalmotilapia boops</i>	1960.9.30 : 1720–24 (FW675)
<i>Ophthalmotilapia ventralis</i>	1950.4.1 : 1291–1465 (FW675)
<i>Xenotilapia boulengeri</i>	1961.11.22 : 290–93 (FW679)
<i>Xenotilapia melanogenys</i>	1960.9.30 : 3419–48 (FW681)
<i>Xenotilapia ochrogenys</i>	1950.4.1 : 4047–136 (FW679)
<i>Xenotilapia ornatipinnis</i>	1960.9.30 : 3685–728 (FW681)
<i>Xenotilapia sima</i>	1961.11.22 : 190–202 (FW680)

#### Lake Fwa

<i>Callopharynx microdon</i>	MRAC 71300 (FW671)
<i>Cyclopharynx fwae</i>	MRAC 71301 (FW671)
<i>Neopharynx schwetzi</i>	MRAC 71290, 76201 (FW671); 71291–99 (FW672)

### A review of group characters for the *Ophthalmotilapia* assemblage

As originally defined by Liem (1981), the *Ophthalmotilapia* assemblage<sup>1</sup> comprised the following genera: *Asprotilapia* Blgr (1901), *Ectodus* Blgr (1898), *Lestradea* Poll (1943), *Cunningtonia* Blgr (1906) and *Ophthalmotilapia* Pellegrin (1904). *Ophthalmochromis* Poll (1956) was shown by Liem (1981 : 210) to be a synonym of *Ophthalmotilapia*, a decision with which I fully agree.

Liem's concept of the OA, and his grounds for considering it a monophyletic group, were based on eight uniquely congruent apomorphic characters present in all the constituent taxa (Liem, 1981 : 207–208). With one possible exception, however, Liem believed that none of these characters is an autapomorphy for the group (Liem's character 2, the outline shape of the palatine bone, is the exception).

The apomorphic status of the eight group-characters was justified by Liem (1981 : 205) on the grounds of their being derived relative to the character state found in various generalized taxa (such as *Astatotilapia burtoni* and *A. elegans*) and in other taxa from Lake Tanganyika.

I have been able to extend Liem's outgroup comparisons to include the cichlid genera of Lakes Malawi, Victoria and Edward, taxa from various river systems and their associated small lakes, and additional genera from Lake Tanganyika itself. Wherever possible, several species of a genus were examined.

The review of the eight OA group-characters which follows takes this extra material into account. It should be noted, however, that the new members of the OA (see p. 262) are, for the purposes of the review, not treated as elements of the assemblage. Thus, unless otherwise indicated, all references to the OA in this section of the paper are to the assemblage as originally defined by Liem.

Since the sequence in which group apomorphies are treated here differs somewhat from that used by Liem (1981 : 207), the number he gave to a character is given, in square brackets, after the number used in this review. The same convention is followed throughout the paper.

(1) [1]. The entopterygoid is widely separated from the palatine (see Liem, 1981 : 205–206, 207; fig. 4; and Figs 1A–F below).

<sup>1</sup>For the sake of brevity, Liem's shorthand term for the assemblage, the OA, will be used in this paper as well.

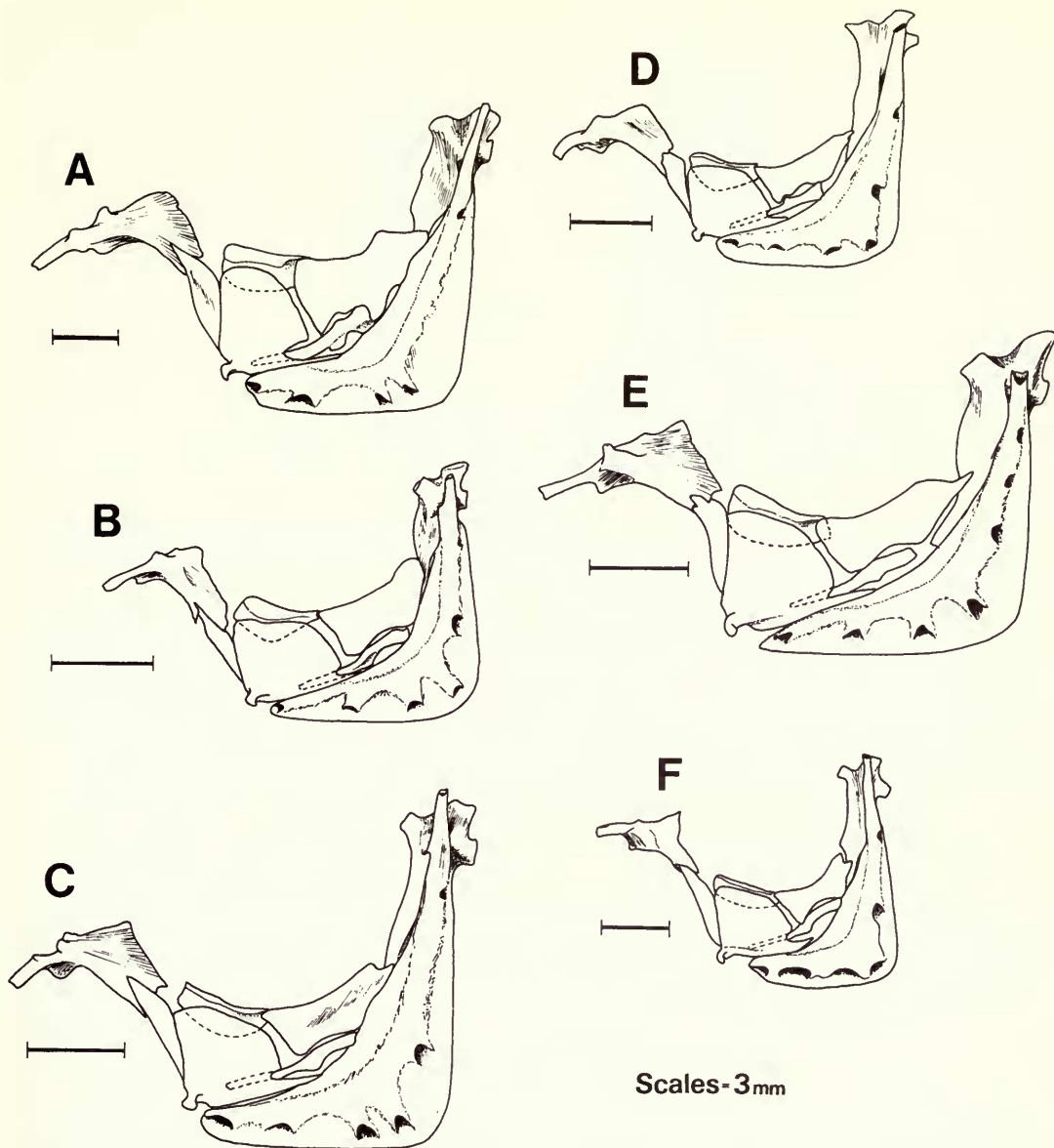


Fig. 1 Suspensoria (left) of: A, *Callochromis macrops melanostigma*; B, *Xenotilapia tenuidentata*; C, *Cyathopharynx furcifer*; D, *Cyathopharynx schoutedeni* (see p. 282); E, *Grammatotria lemairei*; F, *Aulonocranus dewindti*.

As far as I can determine, this character, except for its occurrence in the Malawian genus *Lethrinops* (and those species from Tanganyika which I propose to include in the OA) is unique to the *Ophthalmotilapia* assemblage.

The gap is created, in part, by a reduction in the depth of the entopterygoid, and in part by a reduction of its extension above the quadrate. As a result of these proportional and positional changes, the anterior entopterygoid margin lies below the level of the palatine's posterior margin, and below the upper part of the ectopterygoid as well (with both of which bones it would otherwise articulate). The space between the three bones (that is, the 'gap') is actually filled by dense, translucent connective tissue.

It could be argued (and has been argued by Barel, *pers. comm.*) that the palatopterygoid gap is a correlate of the large and often ovoid eye characterizing all members of the *OA*. This is a complex problem to resolve since the influence of eye size and shape on cranial architecture is the result of several interacting factors, and there are few data available on the dynamics of syncranial ontogeny. In particular we have no information on the influence of ultimate eye size on the ontogeny of the whole suspensorium, of which the palatine and entopterygoid bones are but a part (see below p. 257).

Taking the maximum diameter of the eye (expressed as a proportion of head length) as a measure of eye size it is difficult to find a simple correlation between that ratio and the nature of the palatine-entopterygoid articulation. For example, in *Hemibates*, *Trematocara*, *Reganochromis*, certain '*Limnochromis*' species and in *Perissodus* (all from Lake Tanganyika) the eye is as large as that in members of the *OA*, and the eye in *Trematocara* is as markedly ovoid as it is in any member of the *OA*. Yet, in none of these species is there a palatopterygoid gap. (Recently, Poll (1981) has revised the genus *Limnochromis* which he now divides into four genera. Since several of the older references in the literature are just to the genus *Limnochromis*, I have adopted the convention of referring to the taxon as '*Limnochromis*', except when reference is made to species retained by Poll (1981) in that genus.)

Conversely, in many species of the Malawian genus *Lethrinops* (Fig. 15) there is a palatopterygoid gap (albeit a less extensive one than in some though not all *OA* species), but the eye is smaller than in members of the *OA*.

Since, amongst the taxa with enlarged eyes only the *OA* species have developed a palatopterygoid gap, the gap would seem to be a shared derived character for the assemblage.

That argument would hold even if future research shows the 'gap' to be one of several correlated features associated with the evolution of a large eye. The presence of a gap in *Lethrinops* (which does not have enlarged eyes), on the other hand, fails to support any argument suggesting that eye size and a palatopterygoid gap are necessarily correlated.

- (2) [3]. The slender hyomandibula has a long symplectic process and no, or a very reduced, hyomandibular flange.

On the basis of extensive outgroup comparisons I cannot agree with Liem on the relative length of the symplectic process. In fact, most *OA* species have a process which is no longer than that in *Astatotilapia burtoni*, *A. elegans* (or in other *Astatotilapia* species), or that in other Tanganyika genera (Fig. 2). Unfortunately this character is difficult to quantify and is one affected by the level to which the anterior margin of the hyomandibular flange is produced ventrally. To this extent the apparent length of the process is an optical illusion. It is also affected by the stoutness of the flange which, in this region of the bone, is easily damaged; if partially broken its absence may add to the apparent length of the symplectic process.

As compared with the hyomandibular flange in many taxa (both within and outside Lake Tanganyika) that in all *OA* species is reduced. But, I would question that it is ever absent, even in those species with the greatest reduction in flange area.

A reduction in flange area comparable with that found in *OA* species does occur in several other species as well, and these are mostly taxa with large eyes. Thus, amongst the Lake Tanganyika endemics a reduced *OA*-like flange is found in *Hemibates*, *Trematocara*, *Haplotaxodon*, *Grammatotria*, *Callochromis*, *Xenotilapia*, *Cardiopharynx*, *Cyathopharynx* and *Aulonocara*. In contrast, *Reganochromis calliurus*, whose eye is as large as that in some *OA* species, has a moderately well-developed flange which is larger than that in any *OA* species.

The hyomandibular flange is not reduced in *Lethrinops* (Lake Malawi) nor in any of the species examined whose modal eye size (i.e. eye diameter as a proportion of head length) is less than that of any *OA* species.



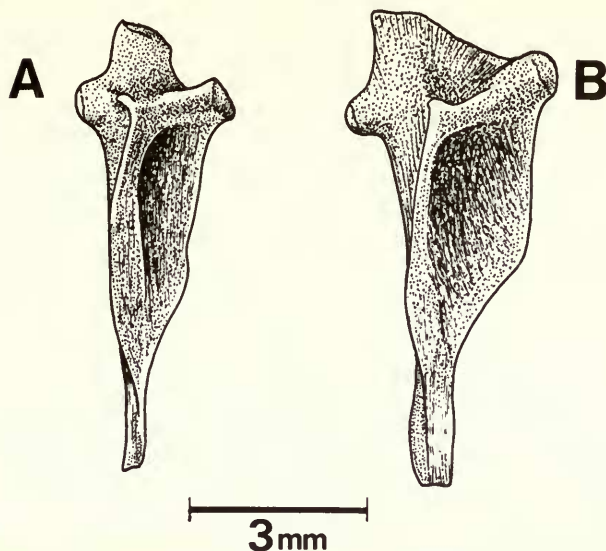


Fig. 2 Hyomandibula (right), in lateral view, of: A, *Ectodus descampsi*; B, *Astatotilapia macropsoides*.

There is thus some suggestion that a reduction in hyomandibular flange area may be correlated with a large eye size. This correlation could result, ontogenetically, from the developing eye preempting some of the space which otherwise would be available for the *levator arcus palatini* muscle whose origin is principally from the flange. It is noteworthy that in those species with a reduced flange, the *levator arcus palatini* has, relatively speaking, a reduced volume, and that its origin has shifted largely to the metapterygoid (Liem, 1981 : 195–6; personal observations).

Incidentally (*pace* Liem, 1981 : 207), in three of the four *Oreochromis niloticus* specimens examined, hyomandibular flange area is proportionately equivalent to that in the *OA* species; in the fourth specimen it is noticeably larger. The two smallest *O. niloticus* (ca. 42 and 52 mm standard length) have the narrowest flanges of the four specimens examined, again suggesting that flange area may be related to eye size since the smallest fishes have proportionately the largest eyes.

(3) [5] The vertical depth of the metapterygoid is shallow.

It is difficult to assess the value of this character as an indicator of phyletic relationships. The metapterygoid is noticeably shallow in all the *OA* species recognized by Liem, and in those which I would add to the assemblage. However, an equally shallow or even shallower metapterygoid is known from several Tanganyika taxa (for example, in species of *Lamprologus*, *Reganochromis*, *Trematocara*, '*Limnochromis*', and also in *Perissodus hecqui*, *P. microlepis* and *P. eccentricus*). In some of these species the eye is large (equivalent in size to those of the *OA* species), in others it is smaller. From this information it is impossible to decide whether a shallow metapterygoid is a correlate of eye enlargement, a homoplastic feature, or one which might be indicative of phyletic relationship at a higher level than that under consideration.

(4) [2] The posterior and dorsal margins of the palatine form a 90° angle. Elsewhere, Liem (1981: 206) expands this statement and notes that 'The 90° posterodorsal angle surrounding a posterodorsal expansion of the palatine is not found in any other Tanganyika cichlids and deviates from the condition in generalized cichlids (e.g. *Astatotilapia burtoni*, Liem and Osse, 1975 and *A. elegans*, Barel, *et al.*, 1976).'

Liem (1981 : 208) places particular importance on this character, considering it as possibly the only autapomorphic feature of the assemblage.

My observations on the *OA* species indicate that the posterodorsal angle is not always rectangular and that it shows some intra- and interspecific variability. Also, I would contest the statement that the *OA* type of palatine shape is not found in other Tanganyika species. It does occur, for example, in *Limnochromis abeelei*, and is closely approached in other species as well. Furthermore it occurs in species outside the lake (e.g. *Astatotilapia macropsoides* [Lakes Edward and George] and in some *Lethrinops* species [Lake Malawi]).

I would agree, however, that the overall type of palatine morphology in *OA* species is relatively uncommon amongst African cichlids, combining as it does a straight or virtually straight posterior margin meeting the dorsal margin at, or almost at, an angle of 90°, and with a posteriorly expanded body of the bone. In combination these features give to the elongate vertical part of the bone a distinctive and near rectangular outline.

Like character (3) [5], the palatine shape is difficult to evaluate as an indicator, or potential indicator, of close phylogenetic relationship. However, since a similarly shaped bone is rarely present amongst taxa other than members of the *OA* (and in those genera where it does occur it is not manifest by all member species), and since non-*OA* taxa with this type of palatine are not closely related to the *OA*, it might well indicate a shared common ancestry for the *Ophthalmotilapia* assemblage.

(5) [4]. The anterior margin of the pterosphenoid is notched.

This character is so widely distributed amongst African cichlids (including the most generalized taxa) that it cannot be treated as an apomorphy at this level of phyletic analysis.

That the notch, or rather the tongue which delimits one aspect of the notch, has not been commented upon before, or been shown in figures of cichlid neurocrania, may well be due to its fragility and hence loss during preparation of the skull. (It is of course absent in some species and is not invariably present in all members of a genus.) Also, the process can be rather small and is then virtually invisible unless the skull is carefully cleaned of connective tissue.

Pace Liem (1981 : 207), the ligament connecting the sclerea with the pterosphenoid or its notch is present in generalized cichlids. In fact, it is present in all the cichlids I have dissected, and also in several other teleostean groups as well (including non-percoids).

(6) Liem's two myological characters, viz. [7] the *transversus dorsalis* is reduced, and [8] the *obliquus posterior* is enlarged, may be taken together.

At the outset of any discussion it must be made clear that neither character is easily assessed, partly because of insufficient comparative data from outgroups, and partly because they are not readily quantified and are thus particularly subjective.

In the discussion which follows, *Asprotilapia* is excluded from any generalizations about the *transversus dorsalis* in the *OA*; *Asprotilapia* does show unequivocally clear-cut reduction of the *transversus dorsalis anterior* and the posterior head of the muscle is not developed at all.

From my observations on dorsal gill-arch muscles in *OA* taxa, and in other cichlids from Tanganyika and elsewhere (including generalized species such as *Astatotilapia elegans*, and 'derived' taxa such as *Bathybates*, *Hemibates* and *Trematocara* (see also Stiassny, 1981), I would not consider the condition of the *transversus dorsalis* or the *obliquus posterior* in *OA* species to be trenchantly distinct. For example, although Liem (1981 : 207) considers the *transversus dorsalis* complex in *OA* species to be reduced relative to that in *A. elegans*, and the *obliquus posterior* to be hypertrophied, I could see no obvious differences when making the same comparisons.

That there are differences in the extent to which these and other dorsal gill-arch muscles are developed amongst African cichlids cannot be denied (see for example Liem, 1973; Liem & Osse, 1975; Stiassny, 1981). But, the differences are rarely trenchant and in some cases

(including manifestly trenchant ones) are the result of environmentally induced individual variations (see Liem & Osse, 1975 : 442, fig. 11; for environmental effects, see Greenwood, 1965).

Thus, until considerably more comparative data are available, and until some means of quantifying apparent differences is employed, the use of relative muscle size would seem to be of very limited value, and could even be misleading. For those reasons I would not use either of the muscle characters in attempting to unravel the phylogeny of the *OA* (except, as noted earlier, with regard to *Asprotilapia*; see below, p. 263).

(7) [6] The operculum has a distinct auricular process.

Although Liem (1981 : 207) notes that a well-developed auricular process occurs on the operculum in several taxa, it is only in *Perissodus hecqui*, '*Limnochromis*' *dhanisi* and the six genera now included in the *OA* (see p. 262) that I would consider the process equivalent to that found in the *OA* species. In all members of the assemblage, the opercular process, although interspecifically variable in form and size, is always a noticeable feature of the bone. That fact, coupled with the infrequent occurrence of a distinct process amongst other genera (and its mosaic interspecific distribution in those taxa), would seem to enhance its value as an indicator of monophyletic origin for the *OA*.

In brief, of the eight supposedly apomorphic characters cited by Liem as suggesting a monophyletic origin for the *OA*, only three would seem to fulfil the necessary requirements for such features, and then mainly because of their unique congruence in the species concerned. The characters, as numbered above, are: the palatopterygoid gap (1), the morphology of the palatine bone (4), and the presence of an auricular process on the posterodorsal margin of the operculum (7).

The remaining characters (i.e. 2, 3, 5 & 6) are either of no value, are possible homoplasies, or cannot be fully evaluated within the scope of our present knowledge.

There are, however, two other characters noted by Liem, and used by him at a different level of universality (the intragroup level), which I consider to be group apomorphies for the whole assemblage. These are:

(8) [15] The morphology of the lachrymal (1st infraorbital) bone.

The lachrymal in members of the *OA* has a very distinctive appearance (see Liem, 1981, fig. 5; and Figs 3A–H), one which, apparently, is not replicated in any other African cichlid. It differs from the generalized condition (as seen, for example, in *Astatotilapia macropsoides*, Fig. 3J) in its overall protraction and relative shallowness. Because the anterior portion is noticeably deeper than the posterior part, the bone has almost the appearance of a short but deep handle extending from its expanded and near rhomboidal anterior region (Figs 3A–H); although the anterior region is much deeper than the posterior part, it is by no means as expansive as it is in the majority of African cichlids.

An elongate lachrymal occurs in a few other taxa (e.g. certain '*Limnochromis*' species; Fig. 3I) but here the bone is uniformly protracted and so lacks the contrast between its shallower posterior third to half and the deeper anterior part, which is so characteristic of the *OA* type lachrymal. Also, in these non-*OA* taxa with an elongate, or relatively elongate lachrymal, the dorsal margin of the bone is but slightly concave, whereas in the *OA* species it is markedly so.

The anterior margin of the lachrymal is straight or very slightly concave, its anteroventral angle produced into a slight but distinctive peak (which is lacking in most species with an elongate lachrymal but is present in some, e.g. '*Limnochromis*' *permaxillaris* and '*L.* *pfefferi*).

When the bone is *in situ* its anterior margin slopes upwards at an angle of 50°–60° to the horizontal (the 'modal' slope in African cichlids would seem to be one close to the horizontal, but there are several and apparently unrelated species where the slope is between 45° and 60°).



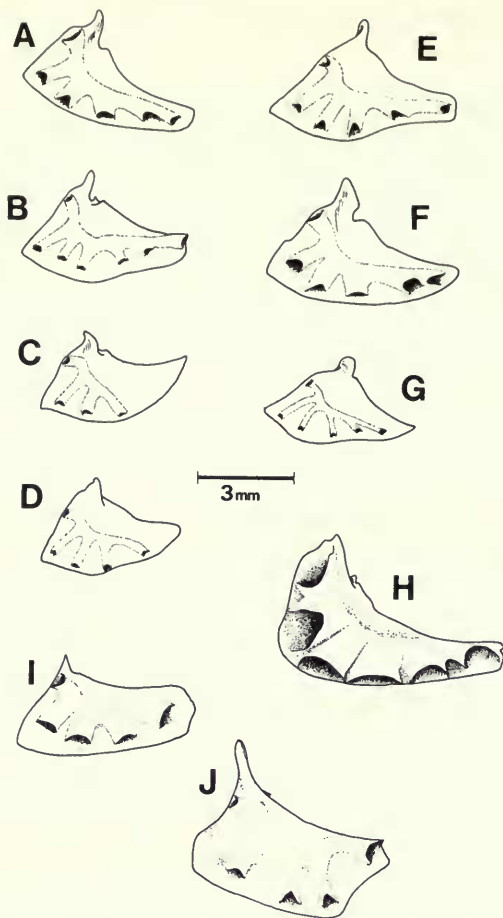


Fig. 3 Lachrymal (left), in lateral view, of: A, *Cyathopharynx furcifer*; B, *Callochromis macrops melanostigma*; C, *Xenotilapia tenuicaudata*; D, *Xenotilapia boulengeri*; E, *Grammatotria lemairei*; F, *Cyathopharynx schoutedeni* (see p. 282); G, *Asprotilapia leptura*; H, *Aulonocranus dewindti*; I, *Limnochromis auritus*; J, *Astatotilapia macropsoides*.

Liem's figure of the *OA* species *Cunningtonia longiventralis* (and his comments on the bone, Liem, 1981 : 206, fig. 5C) represents an unusual condition in that species since the anterior lachrymal margin is shown as markedly concave and aligned almost horizontally. In all 12 specimens I examined, the orientation of the bone and the shape of its anterior margin (including the anteroventral peak) are typically of the *OA* type (see Fig. 4).

There are, with very few individual exceptions, six lateral line canal pores in the lachrymal of *OA* species (but see p. 263 below). The modal number of these pores in all African cichlids is five; the occasional departure from that number seems to be attributable to individual variability. Thus, both in its outline shape (including the anteroventral peak) and in having six lateral line pores, the lachrymal appears to be a unique apomorphic feature for the *OA*.

Liem (1981 : 208) used the presence of an anteroventral peak on the lachrymal as a synapomorphy differentiating *Ectodus*, *Lestradea*, *Ophthalmotilapia* and *Cunningtonia* from *Asprotilapia* which, by implication, lacked this process. In the three specimens of *Asprotilapia leptura* (the sole species) I examined, a typical *OA* peak is present and the outline shape of the bone also conforms with that of other *OA* species (see Fig. 3G).



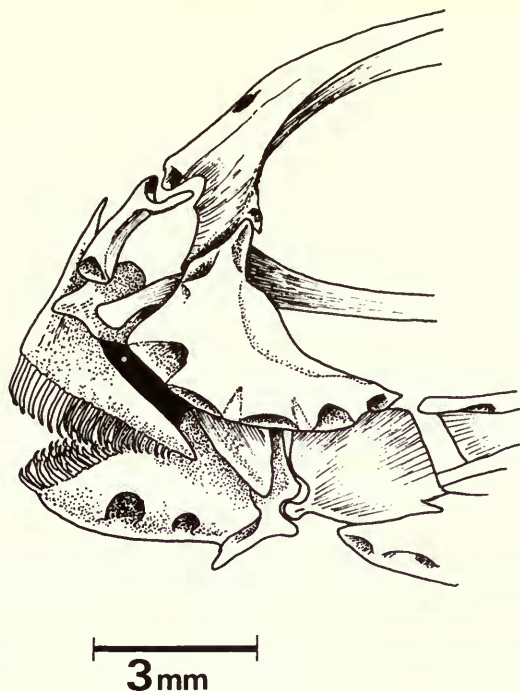


Fig. 4. *Cunningtonia longiventralis*, left lateral view of lachrymal *in situ*.

(9) [9]. The presence on the anguloarticular bone of a well-developed, anteroposteriorly aligned fossa for the insertion of the *adductor mandibulae* muscle  $A_2$ .

This well-developed fossa is noted by Liem (1981 : 195) in his anatomical description of *Ectodus descampsi*, and is illustrated in the six species depicted in his figure 4. Liem did not, however, use the feature as a major apomorphy for the OA as a whole. Indeed, he used the presence of an extensive fossa in *Asprotilapia* as an autapomorphic character for that genus (Liem, 1981 : 208).

In all OA species the fossa is clearly defined, and is limited anteriorly by a prominent, near-vertically aligned ridge on the anguloarticular. The principal surface for muscle insertion is situated on the lateral aspect of the bone, and is thus unlike the generalized condition where it lies on and across the bone's posterior margin. The insertion face, and hence the area of the fossa, varies in size amongst members of the OA. It is largest in *Asprotilapia*, smallest in *Cunningtonia*, with the other species occupying various intermediate positions in the range. Parenthetically, it may be noted that amongst the species I would now include in the OA, the fossa is small in *Cyathopharynx*, of intermediate size in *Xenotilapia* and *Grammatotria*, and largest in *Callochromis*.

Amongst the outgroup taxa examined, an OA type fossa is found only in *Lethrinops* (Lake Malawi), *Trematocara* (Lake Tanganyika), *Chromidotilapia batesi* and *C. kingsleyae* (West Africa) and, in a poorly developed state, in the following Lake Malawi '*Haplochromis*' species '*H.* *prostoma*', '*H.* *johnstoni*', '*H.* *breviceps*' and '*H.* *tetrastigma*'. (For the use of the name '*Haplochromis*' see Greenwood [1979 : 317]).

In all other outgroup taxa examined the *adductor mandibulae*  $A_2$  inserts along the somewhat medially expanded posterior margin of the anguloarticular.

There is no obvious evidence to suggest a recent common ancestry shared by the OA and the *Chromidotilapia* species, nor one between any of the Lake Malawi '*Haplochromis*' and either the OA or the *Chromidotilapia* species.

In the current state of our knowledge one can be less certain about making a similar statement with respect to the *OA* and either *Trematocara* (also from Lake Tanganyika) or the Malawian genus *Lethrinops*. Thus a suspended judgement only can be given on whether the presence of an *OA*-type fossa in these three taxa is a homoplasy, or whether it is a synapomorphy for a group of higher universality than the one under discussion (see also p. 257).

Because the fossa is present in all *OA* species (including the new additions, see below) and because it is congruent with other apomorphic features shared by them, it can, I would consider, be taken as further evidence for the monophyly of the lineage.

To summarise this review of group characters in the *Ophthalmotilapia* assemblage (as defined by Liem, 1981), the congruent apomorphic features are:

- (i) The presence of a palatopterygoid gap (see p. 254)
- (ii) The morphology of the palatine bone (see p. 257)
- (iii) The presence of an auricular process on the opercular bone (see p. 259)
- (iv) The shape of the lachrymal bone (1st infraorbital); see p. 259)
- (v) The presence of a well-defined, laterally placed fossa for the insertion of the *A<sub>2</sub>* *adductor mandibulae* muscle on the anguloarticular bone (see p. 261).

### The *Ophthalmotilapia* assemblage reconsidered

On the grounds of all their constituent species sharing the five features listed above, and because none possesses any feature which might suggest other relationships, six further genera can be included in the *Ophthalmotilapia* assemblage (see Figs 1, 3, 10 and 11).

The new additions are:

- (i) *Xenotilapia* Blgr, 1899 (type species *X. sima* Blgr)
- (ii) *Callochromis* Regan, 1920 (type species *Pelmatochromis macrops* Blgr)
- (iii) *Grammatotria* Blgr, 1899 (type species *G. lemairii* Blgr)
- (iv) *Cyathopharynx* Regan, 1920 (type species *Tilapia grandoculis* Blgr; but see p. 284).
- (v) *Cardiopharynx* Poll, 1942 (type species *C. schoutedeni* Poll)
- (vi) *Aulonocranus* Regan, 1920 (type species *Paratilapia dewindti* Blgr)

Although not apparently relevant to the question of their phyletic relationships, it may be noted that these six genera also share with members of Liem's original *OA* all the other features discussed in the previous section (i.e. characters 2, 3, 5 & 6).

For taxonomic and biological details of these genera and their contained species, reference should be made to Poll (1946 & 1956). Since I can find no grounds for maintaining *Cyathopharynx* and *Cardiopharynx* as separate genera (see p. 282), all further references to these taxa will be made under the name of the senior synonym, *Cyathopharynx*.

Liem (1981 : 208) has already suggested that *Xenotilapia*, *Callochromis* and *Aulonocranus* might be the sister lineage of the *Ophthalmotilapia* assemblage, but he felt that more information was needed before their 'precise relationships' to the others could be determined. His reason for making this suggestion was that all three genera share with the *OA* a palatopterygoid gap and various derived features of the hyomandibula, i.e. characters (1) and (2) above. That the three taxa also shared the other six and supposedly apomorphic features originally used to define the *OA*, was not noted by him.

Although I would be chary of claiming that the 'precise relationships' of *Xenotilapia*, *Callochromis*, *Aulonocranus*, *Grammatotria* and *Cyathopharynx* have been determined, I would submit that an *a priori* case can be established for including them within the *Ophthalmotilapia* assemblage itself, and not just as a sister-group to that lineage.

Before going on to consider intralinear relationships within the expanded *OA*, some comments must be made about certain features in *Aulonocranus* and *Xenotilapia*.

In *Aulonocranus* the lachrymal has the characteristic shape of that bone in other *OA* species (Fig. 3H), but it lacks the anteroventral peak; the anteroventral angle is rounded and

so resembles the condition found in most cichlid taxa. It is possible that this atypical anterior profile might be attributed to the greatly inflated laterosensory canals in the lachrymal of *Aulonocranus*.

In most *Xenotilapia* species too, the lachrymal is atypical for the OA because in these species there are, modally, five and not six openings to the laterosensory canal system (Figs 3C & D). There is, however, considerable inter- and intraspecific variation in pore number; some species have six pores, others only four, and some individuals have a different number of pores on each side of the head. Clearly, pore number is an unstable characteristic in *Xenotilapia*. The genus also differs from all other OA taxa, and all other African cichlids I have examined, in having the posterior opening to the lachrymal laterosensory system positioned below and not opposite the anterior canal opening in the second infraorbital bone.

As in *Aulonocranus*, the outline shape of the lachrymal in *Xenotilapia* is a typical OA one (Figs 3C & D); not surprisingly, considering the number of species (11), there is rather more variation on that basic shape in *Xenotilapia* than in other members of the assemblage.

### Relationships within the *Ophthalmotilapia* assemblage

In its original form, the assemblage was divided into two major sublineages, one comprising only *Asprotilapia leptura*, the other containing the four remaining genera, *Ectodus*, *Lestradea*, *Ophthalmotilapia* and *Cunningtonia* (see Liem, 1981 : 208 & fig. 9).

As defining features for the larger sublineage, Liem employed two supposedly synapomorphic characters: (i) the morphology of the lachrymal, and (ii), the dominance of the A<sub>1</sub> division of the *adductor mandibulae* muscle complex (Liem's characters 15 & 16 respectively).

The *Asprotilapia* lineage was recognized both by the absence of those features, and, more importantly, by its having six presumed autapomorphic characters (see Liem, 1981 : 208).

As argued above (character (8)[15], page 259), the features of the lachrymal must now be considered an apomorphic character for the whole OA (including the new additions and *Asprotilapia* itself).

The muscle character, according to Liem, has two components. First, that the A<sub>1</sub> division of the *adductor mandibulae* has become the dominant component of the complex, its cross sectional area surpassing '... that of the other parts', and second, that '... its origin has expanded ventrally at the expense of the adductor mandibulae part A<sub>2</sub>' (Liem, 1981 : 208).

It is difficult to test the first claim adequately, and my attempts to do so failed to confirm Liem's claims, especially if, as his statement implies, the A<sub>1</sub> division is dominant to both the A<sub>2</sub> and A<sub>3</sub> divisions combined. However, the area of origin of A<sub>1</sub> in the taxon concerned is very clearly greater than that of A<sub>2</sub> when measured by its extent along the vertical arm of the preoperculum (see fig. 6 in Liem, 1981).

When, however, the additional OA taxa are taken into account, the second feature shows a continuous range of variation from a state where the origins of both A<sub>1</sub> and A<sub>2</sub> occupy an approximately equal depth on the vertical preopercular limb, to one where the origin of A<sub>2</sub> is virtually excluded from that limb and thereby is almost confined to the horizontal part of the bone. Furthermore, even within a single genus (as in *Xenotilapia* and *Callochromis*) some species have A<sub>1</sub> and A<sub>2</sub> with almost equal depths of vertical origin (the plesiomorph condition in cichlids), others have the depth of A<sub>1</sub> greater than A<sub>2</sub>, and yet others have A<sub>2</sub> with a much greater vertical depth of origin than A<sub>1</sub> (Fig. 5B). Thus there would no longer seem to be any grounds for maintaining the unity of the *Ectodus-Cunningtonia* sublineage on the basis of its myological characters.

The peculiar arrangement of the *adductor mandibulae* muscles in *Asprotilapia* still stands as a well-defined autapomorphy for the genus. Here, division A<sub>1</sub> is markedly reduced, both in the depth of its origin on the preoperculum, and in its overall bulk (Fig. 5A), a condition not found elsewhere in the OA. Other features, however, suggest that *Asprotilapia* is closely related to some of the newly incorporated members of the assemblage (p. 265).



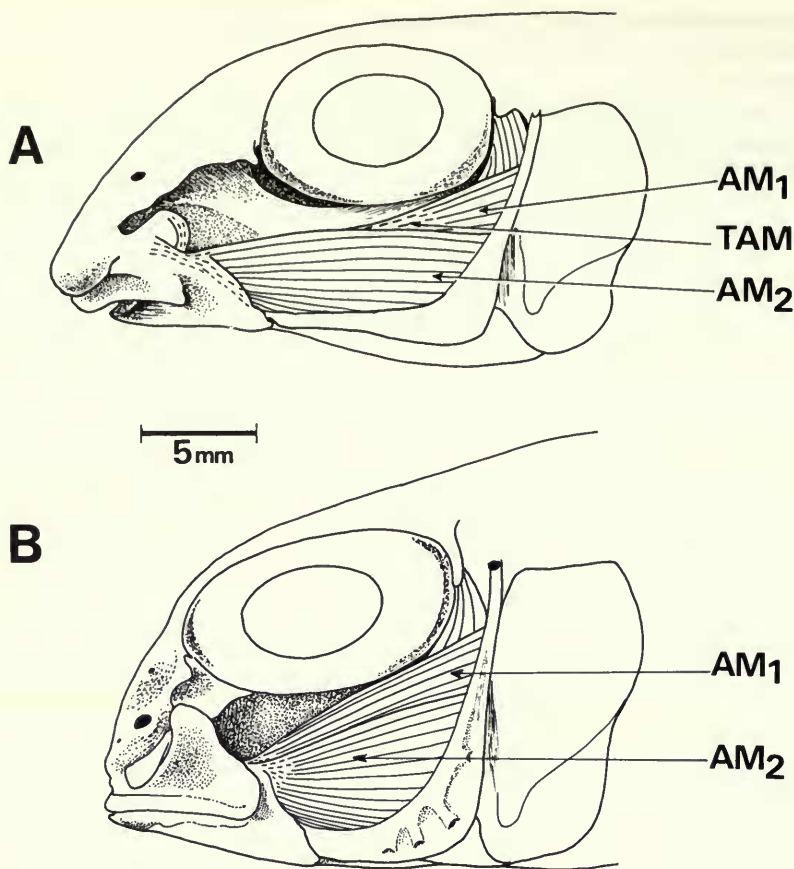


Fig. 5 Superficial adductor mandibulae muscles (left side) of: A, *Asprotilapia leptura*; B, *Xenotilapia sima*. AM<sub>1</sub> & AM<sub>2</sub>: adductor mandibulae divisions 1 and 2; TAM<sub>1</sub>: tendon of insertion for AM<sub>1</sub>.

Although a primary dichotomy within the OA cannot be made on the characters employed by Liem, such a dichotomy can be established on differences in the length of the gut and the manner in which it is arranged within the visceral cavity (see Figs 6 & 7).

Liem (1981: 209; character [19]) used intestinal length to define a group of taxa (*Ophthalmotilapia*, *Cunningtonia* and *Lestradea*) within the original OA, but he did not comment on the spatial arrangement of the alimentary tract in those species.

Within the expanded OA, the member taxa can be grouped into those with an intestinal length less than 3 times the standard length of the body, modally 2.3–2.5 times SL, and those with an intestinal length 3–6 times the standard length.

Species in the first group have the relatively short gut coiled into a few loops whose arrangement is in an essentially anteroposterior direction. In contrast, species with a long gut have the intestine much coiled and the coils are arranged in an essentially transverse direction (see Figs 6 & 7). At first sight this transverse arrangement gives an erroneous impression of the intestine actually being coiled around the stomach (Fig. 7).

A long and complexly coiled gut is a derived feature, occurring in several cichlid lineages. But, since these lineages are not closely related it can be treated as a synapomorphy at the level of universality involved here.



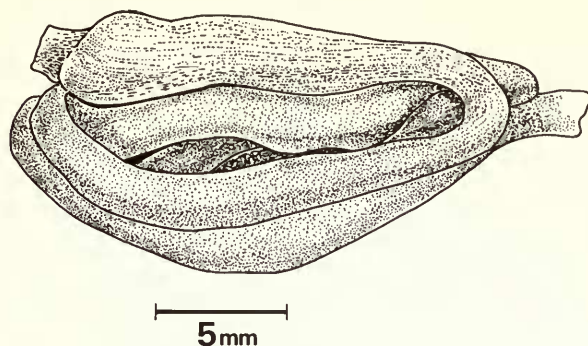


Fig. 6 Alimentary tract (left lateral view) of an *Asprotilapia* subassemblage taxon (*Grammatotria lemairei*).

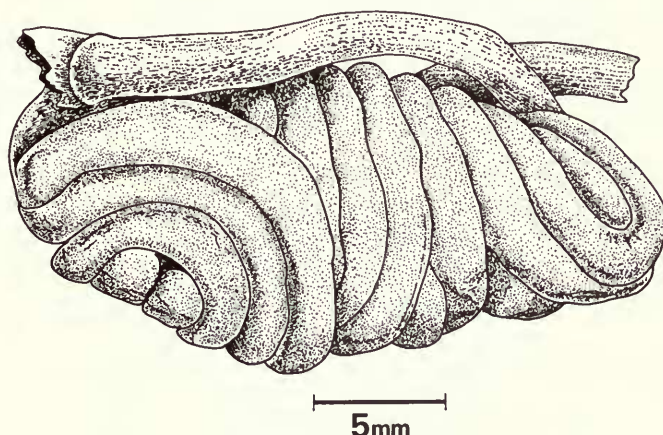


Fig. 7 Alimentary tract (left lateral view) of an *Ophthalmotilapia* subassemblage taxon (*Ophthalmotilapia boops*).

Taxa of the OA belonging to the group with a long and transversely coiled intestine are: *Lestradea*, *Ophthalmotilapia*, *Cunningtonia* and *Cyathopharynx* – hereafter referred to as the *Ophthalmotilapia* subassemblage; their interrelationships will be considered later (see p. 271).

The group with a short and longitudinally coiled intestine comprises the genera *Asprotilapia*, *Callochromis*, *Xenotilapia*, *Grammatotria*, *Ectodus* and *Aulonocara* – hereafter referred to as the *Asprotilapia* subassemblage.

Four genera in the *Asprotilapia* subassemblage, viz. *Asprotilapia*, *Callochromis*, *Xenotilapia* and *Grammatotria*, share an apomorphic feature which suggests their shared common ancestry. This character is the presence of a fully developed pharyngeal hanging pad, with its associated modifications to the superficial anatomy of the gill-rakers; see Figs 8 & 9.

The pad is an hypertrophied and well-circumscribed, forwardly directed, and turgid fold of the buccopharyngeal tissues. It lies immediately anterior to the upper pharyngeal bones and extends forward and downward, as a visor-like projection, for a short distance in front of the first gill-arch. Posterolaterally the pad is fused with the thickened tissue covering the epibranchial gill-rakers of the first gill-arch, but over most of its width the visor-like part is

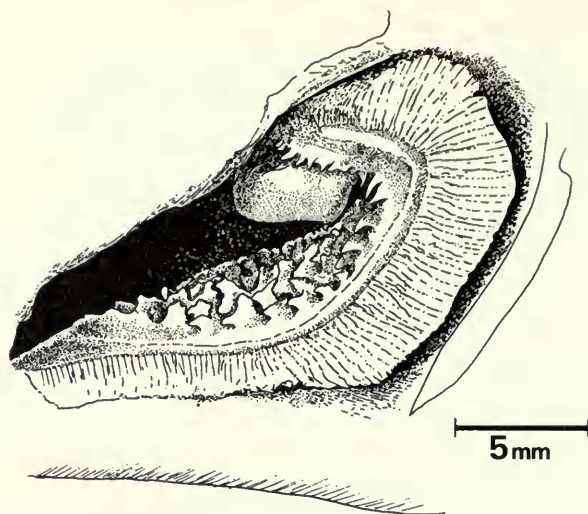


Fig. 8 Pharyngeal hanging pad in *Xenotilapia boulengeri*. Left side, seen from a slightly dorsolateral viewpoint.

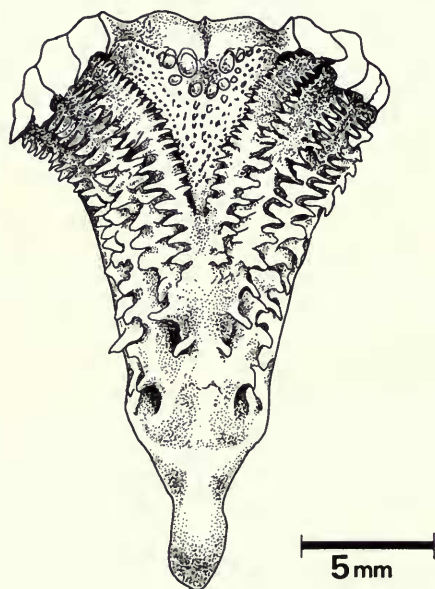


Fig. 9 Ventral portions of the gill-arches, and the lower pharyngeal bone of *Xenotilapia boulengeri*, viewed from above to show the nature of the gill-rakers.

separated from the buccal roof by a distinct transverse groove. This groove is open anteriorly and laterally. In the buccal midline the left and right halves of the visor-like portion are confluent with the buccopharyngeal roof. When the mouth is closed, and the ventral gill-arch skeleton is adducted, the visor occludes the pharynx, leaving only a narrow channel coincident with the medial area of confluence between the two halves of the visor and the buccopharyngeal epithelium.

The pharyngeal surface of the visor is thrown into a large number of broad-based but terminally acute papillae. When the gill-arches are adducted the papillose area is brought into close contact with the upper surface of the cerato- and hypobranchial regions of the gill-arches. These, in turn, are covered by a greatly thickened and soft epithelium. The inner and outer gill-rakers on the ceratobranchial of each arch are joined transversely by anvil-shaped folds of thickened tissue so that, superficially, there appears to be but a single series of rakers, with each raker extending across the breadth of the arch (Fig. 9).

A pharyngeal hanging pad is known from two other, and very dissimilar, African genera, *Chromidotilapia* and *Tylochromis*, and in the South American *Geophagus* (see Trewavas, 1974 : 389–392). Since there are several features strongly indicating that none of these taxa is closely interrelated, and that none is closely related to the *Ophthalmotilapia* assemblage, the repeated occurrence of a hanging pad can only be interpreted as the result of convergent evolution. Any other explanation would be most unparsimonious. It would be equally unparsimonious to assume that its occurrence in four of the OA taxa was the result of independent evolution in each genus. This is particularly so since three of the four genera share another apomorphy, a high number of caudal vertebrae in *Xenotilapia*, *Asprotilapia* and *Grammatotria*, and a second derived character, the shape of the dentary, is shared by *Xenotilapia*, *Callochromis* and *Grammatotria*, of which taxa *Callochromis* alone does not share the vertebral apomorphy.

Thus, on the basis of their all possessing a pharyngeal hanging pad, *Xenotilapia*, *Callochromis*, *Grammatotria* and *Asprotilapia*<sup>1</sup> are taken to form a natural group within the OA. The group can be further subdivided on the distribution within its members of certain other derived features.

*Xenotilapia*, *Callochromis* and *Grammatotria* all have a peculiarly shaped dentary (Fig. 10). When viewed laterally, the dorsal margin of the bone is seen to dip downwards immediately behind the last tooth in the outer row. It continues posteriorly at this lower level until it curves upwards to form the anterior margin of the coronoid process. The alveolar surface is confined to that part of the bone preceding the step, behind which it is edentulous. The dentary of *Asprotilapia* will be discussed below.

This type of dentary, as far as I am aware, is not found in any other cichlid from Lake Tanganyika, or for that matter from Lake Victoria either. It is, however, closely approached by the dentary in the Malawian genus *Lethrinops* and in some '*Haplochromis*' species from that lake. The significance of this similarity, and the occurrence in *Lethrinops* of a palatopterygoid gap, is discussed on page 279.

Within the group comprising *Xenotilapia*, *Callochromis* and *Grammatotria* it is impossible to determine which two genera are the more closely related since no clear-cut linking synapomorphies can be recognized. It is accepted that the diagnostic 'generic' characters for each genus are autapomorphies for that taxon. At present the trio can only be treated as an unresolved trichotomy, but with the suggestion that further research may show *Xenotilapia* and *Grammatotria* to be sister taxa.

*Asprotilapia*, the fourth member of the group, is a most distinctive taxon, in which Liem (1981 : 208) identified six autapomorphies. These must now be reviewed in the context of the expanded *Ophthalmotilapia* assemblage.

As in earlier discussions, Liem's apomorphy number is given in square brackets.

- (i) [9]. The elongate, slender mandible has an expanded adductor fossa for the A<sub>2</sub> division of the *adductor mandibulae* muscle.

As noted earlier (p. 261) the adductor fossa is expanded in several members of the OA, particularly in species of the group to which *Asprotilapia* belongs. However, even amongst those species the fossa is most expansive in *Asprotilapia*.

<sup>1</sup>Microbranchiospines are present in all four of these Tanganyika genera; in this respect they resemble *Tylochromis* and differ from *Chromidotilapia* (see discussion in Trewavas, 1973 : 17 & 1974 : 388).



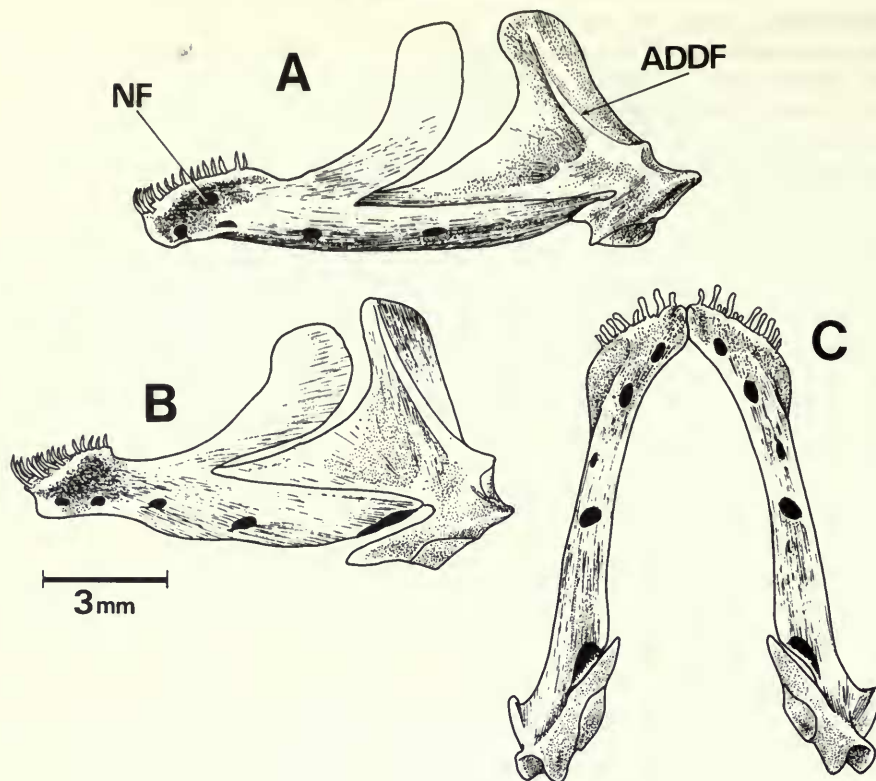


Fig. 10 Dentary and anguloarticular in two species of the *Asprotilapia* subassemblage: A, *Grammatotria lemairei* (lateral view); B & C, *Xenotilapia boulengeri* (lateral and ventral views respectively). ADDF : adductor fossa. NF : nerve foramen.

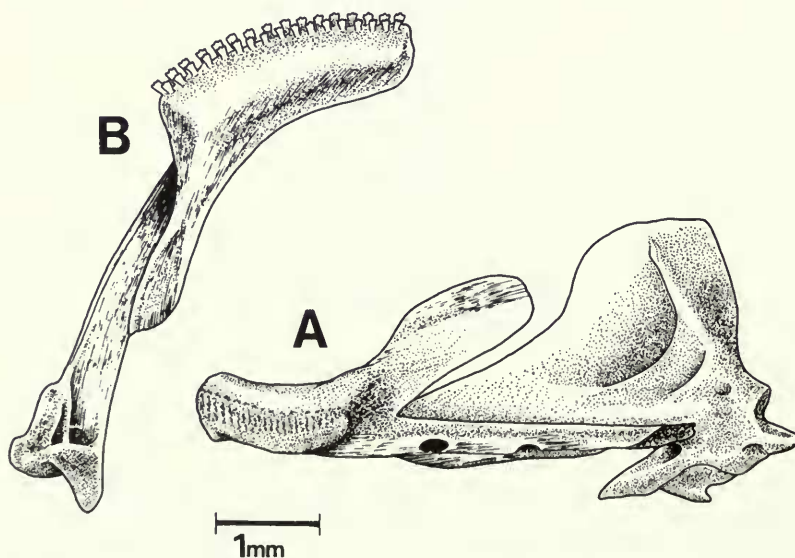


Fig. 11 Left dentary and anguloarticular of *Asprotilapia leptura* in : A, lateral view; B, occlusal view. In B the teeth have been restored (based on a spirit specimen), but in A only the tooth scars are shown.



The mandible is not, in my view, especially elongate, particularly when it is compared with that element in other members of the *Asprotilapia* subassemblage (cf. Figs 10 & 11). Its gross morphology differs from that in *Xenotilapia*, *Callochromis* and *Grammatotria* since it lacks a 'stepped' alveolar margin, and because each ramus of the jaw has a more abrupt and stronger medial curvature towards the symphysis. Also, in *Asprotilapia*, immediately before the dentary curves inwards, the alveolar surface is produced laterally so as to form a noticeable, shelf-like overhang of the underlying ramus (Fig. 11).

Overall, the dentary in *Asprotilapia* bears a fairly close resemblance to that bone in *Labeotropheus* of Lake Malawi, a resemblance enhanced by the tricuspid, slender-necked, procumbent and movably implanted teeth present in both genera. *Asprotilapia* has, however, a shallower dentary, and the anguloarticular is taller and more expansive than in *Labeotropheus*. Parenthetically it may be noted that *Asprotilapia*, like *Labeotropheus*, has an enlarged and similarly shaped cartilaginous meniscus underlying the premaxillary ascending process, and a similar fleshy medial projection overlying the broad palato-premaxillary ligaments. Observations made from radiographs of the two species, and from manipulation of preserved specimens, indicate that the protrusile mechanisms in the two species are very similar. There are, however, no reasons to doubt that these similarities should be treated as homoplasies.

(ii) [10]. The posterior head of the *transversus dorsalis anterior* muscle is absent.

This seems to be a clear-cut autapomorphy, but should be checked in more examples than the single specimen available to Liem and myself.

(iii) [11]. Lateral ethmoids greatly enlarged.

This again is an apparently good autapomorphy.

(iv) [12]. Interorbital width greatly reduced.

The interorbital width is reduced in some *Xenotilapia* species, but in none is it as narrow as in *Asprotilapia*.

(v) [13]. The reduced articular process of the premaxilla is in a more forward position.

There is considerable and continuous variation in the relative position of this process in *Xenotilapia* species, and indeed within the taxa of the entire *OA*. It would not, therefore, seem to be a character of particular value.

(vi) [14]. The greatly enlarged cranial condyle and the premaxillary process constitute the bulk of the maxilla.

The maxilla of *Asprotilapia* is less outstanding when compared with that bone in other members of the subassemblage, especially *Xenotilapia* (Fig. 12). In *X. boulengeri*, for example, the process is larger than in *Asprotilapia*. The cranial condyle, however, is largest in *Asprotilapia* and, as compared with all other *OA* species, the whole bone is relatively foreshortened.

In the context of the expanded *OA*, I would consider that at least three of the autapomorphies originally proposed (i.e. nos. i, ii and iii above) retain their validity (if, that is, the apomorphic features of the lower jaw are interpreted as has been done here).

Although not listed as an autapomorphy by Liem (1981), the peculiar condition of the  $A_1$  division of the *adductor mandibulae* muscle in *Asprotilapia* would seem deserving of that status. In *Asprotilapia*, as compared with all other *OA* taxa,  $A_1$  is a very short and narrow muscle with an extremely long tendon of insertion (Liem, 1981; fig. 6; also Fig. 5), and an area of origin much smaller in all respects than that of the  $A_2$  division. No other species in the *OA* has this arrangement of the *adductor mandibulae* muscles.

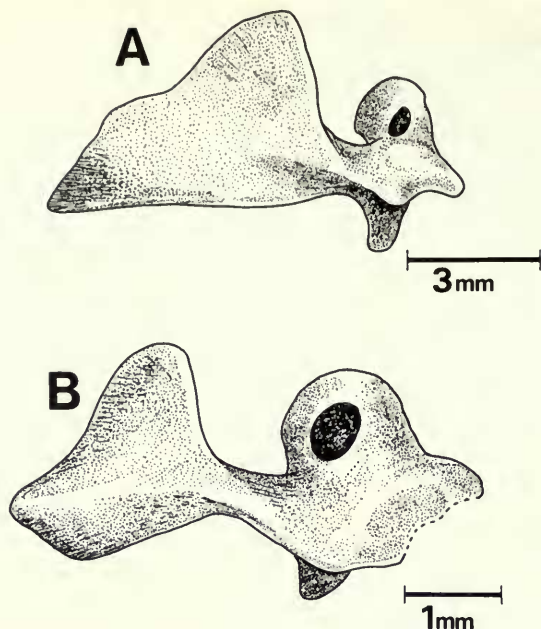


Fig. 12 Right maxilla, in lateral view, of: A, *Xenotilapia boulengeri*; B, *Asprotilapia leptura* (the damaged ventral margin of the premaxillary saddle is indicated by a broken line).

When commenting on the unusual  $A_1$  muscle in *Asprotilapia*, Liem (1981:203) makes particular reference to a tendon stemming from the muscle's principal tendon of insertion, and which joins the tendinous part of adductor division  $A_{10}$ . This emphasis might give an impression that the vertically directed interconnecting tendon is a unique (or unusual) feature of *Asprotilapia*. That is not so because the tendon is present in all cichlids whose jaw musculature has been examined (see for example Liem & Osse, 1975: fig. 6; Stiassny, 1981: 80, and figs 8 & 11 [tA<sub>1</sub>,b]; also personal observations on species other than those studied by these authors). *Asprotilapia* is, however, unusual in having a discrete, ligament-like condensation in the connective tissue between the premaxilla and dentary, inserting on the lateral (and not the medial) face of the premaxilla.

Interestingly, despite the resemblances in lower jaw morphology between *Asprotilapia* and *Labeotropheus* (see above p. 269), the pattern of adductor muscles in the two genera is quite different. *Labeotropheus* has the typical generalized cichlid arrangement.

The various autapomorphies of *Asprotilapia* serve to indicate the taxon's isolation within its group. For the moment it can only be treated as the sister taxon to the other three genera (i.e. *Callochromis*, *Xenotilapia* and *Grammatotria*) combined.

The two remaining taxa in the *Asprotilapia* subassemblage (see p. 265), *Ectodus* and *Aulonocranus*, are 'interrelated' only at the level of their sharing with their supposed sister-group, *Asprotilapia*, *Callochromis*, *Xenotilapia* and *Grammatotria*, the plesiomorphic feature of a short intestine. With one possible exception, neither *Ectodus* nor *Aulonocranus* has any uniquely shared derived features suggestive of their recent common ancestry.

The exceptional feature concerns the marked elongation of the first, and to a lesser extent the second pelvic fin rays in adult males. In *Aulonocranus* the first ray extends to about the middle of the anal fin, and in *Ectodus* to a point beyond its spinous part, but never as far as the middle of the fin. Other members of the *Asprotilapia* subassemblage have variously modified relative proportions of different pelvic fin rays (see Poll, 1956) but none has the first ray elongated to the degree found in *Ectodus* and *Aulonocranus*. The significance of this feature is, however, somewhat questionable (see p. 272).

In Liem's scheme (1981 : 208–9, fig. 9), *Ectodus* was allied with *Lestradea*, *Ophthalmotilapia* and *Cunningtonia* (now considered to be a separate sublineage, see below) and not with *Asprottilapia*. Liem's grounds for this alliance were based on *Ectodus* sharing two apomorphic characters with *Lestradea*, *Ophthalmotilapia* and *Cunningtonia*, namely a distinct antroventral process on the lachrymal bone, and a dominant  $A_1$  division in the adductor mandibulae muscle complex.

As was argued above (pp. 262–263) the former character is one shared by all members of the OA (except *Aulonocranus*) and the latter is a variable feature of little value as an indicator of relationships within the OA.

*Aulonocranus* was not included in the original OA, although Liem (1981 : 206 & 208) did suggest that it might be related to that assemblage.

The genus is readily identified by one outstanding apomorphy, the hypertrophy of its cephalic laterosensory canal system, and as a probable correlate, the enlarged saccular bulla in the basioccipital and prootic bones.

*Ectodus* has one autapomorphy, viz. the vertical and horizontal limbs of the preoperculum are of equal or almost equal length (see Liem, 1981 : 209). Liem also ranked the enlarged saccular bulla as an autapomorphy, but the bulla is enlarged to an equal extent in *Lestradea* and *Ophthalmotilapia* amongst members of the original OA, and in *Aulonocranus* and *Cyathopharynx* among the new additions to the assemblage. Indeed, apart from *Callochromis*, *Xenotilapia* and *Grammatotria* the saccular bulla is noticeably enlarged in all OA species, the degree of enlargement showing a continuous increase from the condition in *Asprottilapia* through to that in *Aulonocranus*, with *Lestradea*, *Ectodus* and *Ophthalmotilapia* all close to *Aulonocranus*.

Turning now to the second lineage of the primary dichotomy, the *Ophthalmotilapia* subassemblage (p. 265), one again finds difficulty in establishing intragroup relationships, but little difficulty in recognizing autapomorphies for the constituent genera, viz. *Lestradea*, *Ophthalmotilapia*, *Cunningtonia* and *Cyathopharynx*.

Since *Lestradea* lacks the various derived features shown by its congeners in the subassemblage it would appear to be the plesiomorph sister taxon to the other three genera combined.

Liem (1981 : 209) singled out two autapomorphies for *Lestradea* (i) the edentulous anterior process of the lower pharyngeal bone is only half as long as the toothed part (his apomorphy 20), and (ii), the body of the maxilla is stout, and has a prominent postmaxillary process (his apomorphy 21).

I cannot agree with Liem's statement about the relative proportions of the anterior process of the lower pharyngeal bone. The *Lestradea* specimens I have examined all have this process as long as, or almost as long as the toothed part, a condition approaching that in *Ophthalmotilapia* and *Cunningtonia*. This condition must be considered derived relative to that in *Astatotilapia* and many other African cichlids. In these various taxa the edentulous anterior process of the bone is indeed half or less than half as long as the toothed part.

The body of the maxilla in *Lestradea* is stout and the posterior process is prominent, but in both features the bone does not differ from the maxilla in *Ophthalmotilapia* where the process is a little less prominent. A relatively short maxilla with a prominent posterior process is, it would seem, a common feature in the whole *Ophthalmotilapia* assemblage.

*Cyathopharynx* is readily distinguished by its autapomorphous lower pharyngeal bone (Fig. 23), with its deeply concave occlusal surface, heart-shaped dentigerous area, and greatly inflated body below that surface. There are, however, no synapomorphies (except group ones) shared by *Cyathopharynx* and any other member of the subassemblage.

Liem (1981 : 209) recognized three synapomorphies which suggested to him that *Ophthalmotilapia* and *Cunningtonia* were members of a monophyletic unit. The presumed synapomorphies were (i) jaw teeth with long stalks, and movably implanted, (ii) the first pelvic ray greatly elongate (Liem's apomorphies 22 & 23 respectively), and (iii) the posterior margin of the vertical preopercular limb is straight and forms a 90° angle with the horizontal limb.



The teeth in all members of the *OA* (*sensu lato*) are movably implanted, and in all species the teeth could be described as having 'long stalks', albeit with specifically distinct but varying degrees of slenderness. For example, in both these features the outer jaw teeth in *Ophthalmotilapia* are very like those in *Lestradea*, but those in *Cunningtonia* have a much more slender and elongate neck than do the teeth in any other *OA* species.

The first and second pelvic rays are elongate (much more so in males than in females) in both *Ophthalmotilapia* and *Cunningtonia*, with, in the former, the first ray somewhat longer than the second. But, when other species in the expanded *OA* are taken into account one finds that the condition of the two rays in *Cyathopharynx furcifer* is like that in *Cunningtonia longiventralis*, and that *Aulonocranus* also has elongate rays but which extend only to the middle of the anal fin base and not to the posterior margin, or slightly beyond, as they do in *Cunningtonia* and *Cyathopharynx furcifer*. *Cyathopharynx schoutedeni* has elongate first and second pelvic rays too, but in this species it is the second ray which is the longer and, unlike the elongate first ray in *C. furcifer*, it extends posteriorly only a short distance beyond the spinous part of the anal fin.

Thus it is difficult to treat marked elongation of the first, or first and second pelvic rays as a synapomorphy for *Ophthalmotilapia* and *Cunningtonia*. That it is a character showing continuous variation and one that is incongruent with other apomorphies would also preclude its use as an indicator of recent shared common ancestry for the genera exhibiting it, namely *Aulonocranus*, *Ophthalmotilapia*, *Cunningtonia* and *Cardiopharynx* (see below).

Some comment on the spatulate, or bifid tips to the first ray in males of *Ophthalmotilapia* species would be appropriate here.

The feature appears to be a unique apomorphy for *Ophthalmotilapia*, indeed it is one of the reasons given by Liem (1981:210) for synonymizing *Ophthalmochromis* with that genus. Spatulate tips have not been mentioned in the formal descriptions of any other species, nor have I seen such modifications in any of the taxa, other than *Ophthalmotilapia*, which I have examined. However, Brichard (1978:187) describes the pelvic fin in *Cyathopharynx furcifer* as having '... a long filament tipped with a yellow double spatula'. On page 190 of the same book he comments on 'The ventral filaments, reaching the end of the anal fin are each tipped with a double yellow-orange spatula'. Finally, Brichard (1978:148 & 149) provides two illustrations of a live individual (or individuals) showing what certainly looks like a spatulate tip to the protracted pelvic fin rays.

Brichard is an experienced underwater-naturalist and one is hesitant to suggest he has misidentified his material. On the other hand, in his description (Brichard, 1978:326) of *Ophthalmotilapia ventralis* (as *Ophthalmochromis ventralis*) he remarks that 'The males ... have very long pelvic filaments also forked like *O. nasutus*, but the tips are **without spatulae** (although they are pale yellow like those of *O. nasutus*)'; bold type added. Clearly there is some terminological confusion here since none of the male *O. ventralis* specimens I have examined, or those which have been described elsewhere, lacks well-defined spatulae.

The tips of the elongate pelvic rays in *Cyathopharynx* are brightly coloured, and seem to serve the same ethological function as the spatulae in *Ophthalmotilapia*. Perhaps the confusion stems from that colour similarity rather than a structural one? Until spatulate *Cyanopharynx* are described formally, the uncertainty will remain.

In itself, very marked elongation of the first and second pelvic rays is a derived feature (see below), but in the context of the *OA* it is not clear at what level of universality it can be recognized as a synapomorphy. For example, if used to unite *Aulonocranus*, *Cyathopharynx*, *Ophthalmotilapia* and *Cunningtonia*, pelvic fin length would be incongruent with the group synapomorphy of an elongate and complexly folded intestine shared by all except *Aulonocranus*, which has a short and simply folded intestine. If, on the other hand, because of its short gut *Aulonocranus* was taken to be the plesiomorph sister taxon of the others, then where would *Lestradea* which has a long gut but short pelvic fins be placed?

The problem is further compounded by *Ectodus* which has a short and simply folded gut but elongate first and second pelvic rays produced to a degree almost comparable with those in *Aulonocranus*.

In no case are there any known synapomorphies which are uniquely congruent with protracted pelvic fin length, and which would thereby establish a strong case for arguing that the gut character is a homoplasy. Finally, it must be recalled that some relative elongation of the first and second pelvic rays is of relatively common occurrence in African cichlids (see Greenwood, 1981), and that the degree of elongation must be treated as a continuous variable, albeit one rarely reaching the extremes found in *Cunningtonia* and *Ophthalmotilapia*.

Liem's third synapomorphy (involving the shape of the preoperculum; see page 271) is also difficult to substantiate, particularly in the context of the expanded OA. In all constituent species of the OA *sensu lato* the vertical and horizontal limbs of the preopercular bone meet at, or very nearly at, a right angle, and in all except *Ophthalmotilapia* and *Cunningtonia* the posterior margin of the vertical limb curves inwards for a short distance near its dorsal extremity. Because *Ophthalmotilapia* and *Cunningtonia* have the bony flange behind the vertically aligned laterosensory canal tube narrowing imperceptibly, rather than abruptly, the entire posterior margin of the preoperculum does give the impression of being straight in these two species. The difference between the two types of posterior margin is, however, very slight and is almost obliterated by the condition in *Cyathopharynx*. Here the dorsal extremity of the margin is slightly indented, but less noticeably so than in most other OA taxa.

Thus, of the three apomorphies under review, only the nature of the preopercular margin, a not particularly trenchant character, would seem to be a synapomorphy linking *Ophthalmotilapia* and *Cunningtonia*.

On the morphological evidence alone, it is thus impossible to hypothesize precise intragroup relationships for the *Ophthalmotilapia* subassemblage, except to note that on a simple summation of derived features *Lestradea* would seem to be the most plesiomorph taxon. At the generic level the other taxa are readily identified by their particular autapomorphies (see below).

It is possible that these currently obscure and therefore uncertain intralineage relationships will be clarified when more data are available on the breeding habits of its constituent species. Brichard (1978 : 108), for example, groups *Cyathopharynx* with *Ophthalmotilapia* as polygamous spawners in which there is no contact between the sexes at the nest site. The import of Brichard's statement is not really clear, and the phyletic importance of most ethological characters still awaits evaluation. Nevertheless it is suggestive that Brichard did single out these taxa as forming a distinctive reproductive class.

Returning now to the autapomorphic features of the genera constituting the subassemblage, one finds that *Ophthalmotilapia* (*sensu* Liem, 1981 : 210) is distinguished by the bifid spatulae in which each elongate first pelvic ray terminates, and the subdivision of the *retractor dorsalis* muscle of the upper gill-arches into two distinct heads (see Liem, 1981 : 201, fig. 8D).

*Cunningtonia* has as its principal autapomorphies the nature of its oral dentition, the stout foreshortened dentary (Fig. 13) and the stout premaxilla.

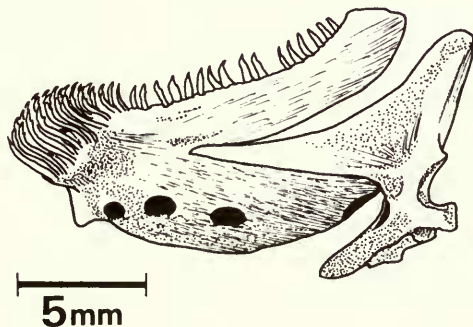


Fig. 13 Left dentary and anguloarticular of *Cunningtonia longiventralis* in lateral view.

Most of the jaw teeth are very slender and tall, with strongly recurved, tricuspid and broad crowns. The teeth are arranged in wide bands over the entire alveolar surface of the premaxilla and on the transverse part of the dentary, but on the lateral alveolar surface the teeth are much stouter and are unicuspid.

The palatine of *Cunningtonia* is also unique in having its facet for articulation with the lateral ethmoid expanded medially into a shelf-like projection. When viewed from the side, especially in specimens prepared as alizarin transparencies, the shelf has a spine-like appearance (see Liem, 1981 : 210; apomorphy 26).

Liem considered that the symplectic in *Cunningtonia* was '... very elongate' (his apomorphy 28), but I find that it is of virtually equal relative length in all members of the OA.

In *Cyathopharynx* the principal autapomorphy is the peculiar, heart-shaped and deeply concave denticerous surface of the lower pharyngeal bone and, of course, the correlated changes in the shape of the upper pharyngeal elements (see p. 288).

### The nature of the apophysis for the upper pharyngeal bones in the *Ophthalmotilapia* assemblage

Like Liem (1981), I have not taken into account the nature of the pharyngeal apophysis when analysing intragroup relationships amongst members of the OA (see Greenwood, 1978, for an evaluation of this character in determining phyletic relationships; also Fryer & Iles, 1972 : 504 *et seq.*).

Based on material examined personally, the distribution of apophyseal types (defined as in Greenwood, 1978) within the two major subassemblages of the OA is as follows:

<i>Asprotilapia</i> subassemblage			<i>Ophthalmotilapia</i> subassemblage		
Hap. <sup>1</sup>	Troph.	Tilapia	Hap.	Troph.	Tilapia
<i>Callochromis</i>	<i>Xenotilapia</i> (a few spp.)	—	—	<i>Cyathopharynx</i>	<i>Lestradea</i>
<i>Xenotilapia</i> (most spp.)	<i>Aulonocranus</i>	—	—		<i>Ophthalmotilapia</i>
<i>Grammatotria</i> *	<i>Ectodus</i>	—	—		<i>Cunningtonia</i>

<sup>1</sup>Hap. = *Haplochromis* type; Troph. = *Tropheus* type; Tilapia = *Tilapia* type.

\*In all specimens the apophysis is of the *Haplochromis* type on one side, and the *Tropheus* type on the other.

It is interesting that no true *Tilapia* type apophysis occurs amongst members of the *Asprotilapia* subassemblage, but that three of the four taxa in the *Ophthalmotilapia* subassemblage do have an apophysis of that type. In contrast, a *Haplochromis* type apophysis occurs in three members of the *Asprotilapia* subassemblage but not in any taxa of the *Ophthalmotilapia* subassemblage.

It must be borne in mind, however, that the *Tropheus* apophyseal type is structurally intermediate between the *Haplochromis* and *Tilapia* types (see Greenwood, 1978) and that in the *Asprotilapia* subassemblage certain taxa have more than one type of apophysis. Indeed, the three specimens of *Grammatotria lemairei* examined have a *Haplochromis* type apophysis on one side of the skull and a *Tropheus* type on the other.

It is also interesting to note that if the *Tropheus* category (of Greenwood, 1978), which Regan did not recognize, is ignored and the taxa in that category are returned to the one in which they were placed by Regan (1920), then the entire *Asprotilapia* subassemblage is of the *Haplochromis* type, and the *Ophthalmotilapia* subassemblage becomes exclusively of the *Tilapia* type.



Such a pattern might well be taken to argue against my earlier criticisms of the pharyngeal apophysis as an indicator of phyletic relationships at a high level of universality (Greenwood, 1978) and that, on the contrary, African cichlids can be divided into '*Tilapia*' and '*Haplochromis*' supralineages as suggested by Regan (1920).

If the latter argument is accepted, then the synapomorphies delimiting the *Ophthalmotilapia* assemblage as a whole must be considered as homoplasies developed independently in the two subassemblages recognised here. That assumption would produce a scheme of relationships less parsimonious than the one proposed above and earlier by Liem (1981). Also, the existence of intermediate conditions (i.e. the *Tropheus* type) in the structure of the apophysis, and of other cases where a classification based on apophyseal structure is incongruent with different and apparently synapomorphic characters (see Greenwood, 1978; Liem & Stewart, 1976) would seem to support the rejection of apophyseal structure as an indicator of phyletic relationships at the level proposed by Regan.

### A review of other schemes of relationship suggested for members of the *Ophthalmotilapia* assemblage

Regan (1920 : 52) did not present detailed arguments for his views on the interrelationships of the Lake Tanganyika genera, which were strongly influenced by his assumption of there being a fundamental dichotomy of African cichlids into those with a '*Tilapia*' type apophysis, and those with a '*Haplochromis*' type (see above). As a result of this basic difference in approach, it is difficult to make direct comparisons between Regan's ideas and those put forward in this paper. However, some comments can be made on certain of Regan's suggested relationships involving *OA* members and taxa outside that assemblage.

For example, *Ophthalmotilapia* was grouped with *Cyathopharynx*, *Cunningtonia*, *Asprotilapia*, *Petrochromis* and the Malawian genus *Petrotilapia* (then considered a species of *Petrochromis*); furthermore, Regan suggested that *Ophthalmotilapia* was closely related to *Limnotilapia* (now synonymised with *Simochromis*, see Greenwood, 1979) and that it had '... given rise to *Cyathopharynx*'.

*Petrochromis* and *Petrotilapia* were included in this grouping because, in their dental morphology and pattern, they are strikingly similar to *Cunningtonia* (see p. 280 below).

No reasons were given for including *Asprotilapia*, a taxon quite unlike the others in its gross morphology and in its dentition; presumably the reason lay in Regan's (1920 : 42) belief that the 'Skeleton (is) essentially similar to that of *Ophthalmotilapia ventralis*...'. The skeletal features noted by Regan (1920 : 41 & 42) were, it should be emphasised, not those used in this paper; most can be treated as plesiomorph characters when used at the level of analysis involved here.

Presumably it was the same suite of skeletal characters which led Regan to suggest a close relationship between *Limnotilapia* (i.e. *Simochromis*) and *Ophthalmotilapia*, a relationship which I cannot accept since '*Limnotilapia*' apparently shares no derived features with any members of the *OA*.

*Ectodus* (as a putative ancestral morphotype) was grouped by Regan (1920 : 53) with *Callochromis*, *Xenotilapia* and *Grammatotria*, the taxa being given that order of increasing morphological derivation. Again no detailed reasons are given for this grouping, save that all its taxa have a '*Haplochromis*' type pharyngeal apophysis and small conical teeth. In effect, however, it approximates closely to the arrangement proposed in this paper.

Regan (1920 : 53) also included, albeit implicitly rather than explicitly, *Aulonocranus* and *Trematocara* with those genera listed in the previous paragraph. The association of *Aulonocranus* with *Trematocara* was, presumably, based on both genera having hypertrophied cephalic laterosensory canal systems (Regan, 1920 : 47); no other relationship with *Aulonocranus* was suggested, save that it is 'Intermediate between *Haplochromis* and *Trematocara*.' The linking of *Aulonocranus* and *Trematocara* with the *Ectodus*-*Grammatotria* group (see above) was apparently based on the common possession of small conical teeth and a '*Haplochromis*' type of pharyngeal apophysis.

That Regan did not consider there to be any relationship between his *Asprotilapia-Ophthalmotilapia* and his *Ectodus-Grammatotria* (+ *Aulonocranus*) groups is doubtless due to his basic assumption that the endemic genera of Lake Tanganyika were derived from '...two ancestral types, one nearly related to *Limnotilapia* and the other to *Haplochromis*' (Regan, 1920 : 53).

After Regan's initial analysis of the Tanganyika cichlids, no further attempt to interrelate the endemic genera of the lake was made for more than fifty years. In 1972 Fryer & Iles paid considerable attention to this problem, in particular to the assumption that there was a basic diphyletic origin of the flock. However, despite their professed uncertainty about the value of the pharyngeal apophysis as an indicator of phyletic relationships, Fryer & Iles (1972 : 506, fig. 337) virtually followed Regan's (1920) scheme. They were, of course, able to include three genera described since that time, namely *Lestradea*, *Cardiopharynx* and *Ophthalmochromis*. *Cardiopharynx* is now considered a synonym of *Cyathopharynx* (see p. 282) and *Ophthalmochromis* was synonymised with *Ophthalmotilapia* by Liem (1981 : 210–211).

As would be expected, Fryer & Iles considered *Ophthalmochromis* and *Cardiopharynx* to be the sister taxa of *Ophthalmotilapia* and *Cardiopharynx* respectively. Interestingly, they associated *Lestradea* with *Asprotilapia*, *Cunningtonia* and the *Ophthalmotilapia-Ophthalmochromis* pair, but gave no reasons for doing so. Their tentative alliance of *Cyathopharynx*+*Cardiopharynx* with *Lobochilotes* and *Limnotilapia* is not explained either, and only partly follows Regan who implied some relationship between *Limnotilapia* and *Lobochilotes*, but also included *Gephyrochromis*, *Simochromis* and *Tropheus* in the same group—again without a detailed explanation (Regan 1920 : 52). I can find no synapomorphic characters to support the idea of a close relationship between *Lobochilotes* and any member of the *Ophthalmotilapia* assemblage.

Like Regan, Fryer & Iles (1972 : fig. 337) treat *Aulonocranus* and *Trematocara* as close relatives, but give the two genera an origin separate from that of the taxa currently grouped in the OA.

*Leptochromis* (now renamed *Reganochromis*, see Whitley, 1928), a genus not mentioned in Regan's analysis, is included by Fryer & Iles as a member of their *Ectodus*, *Callochromis*, *Xenotilapia* lineage, but again no reasons are given. This suggested relationship is discussed on p. 278 below.

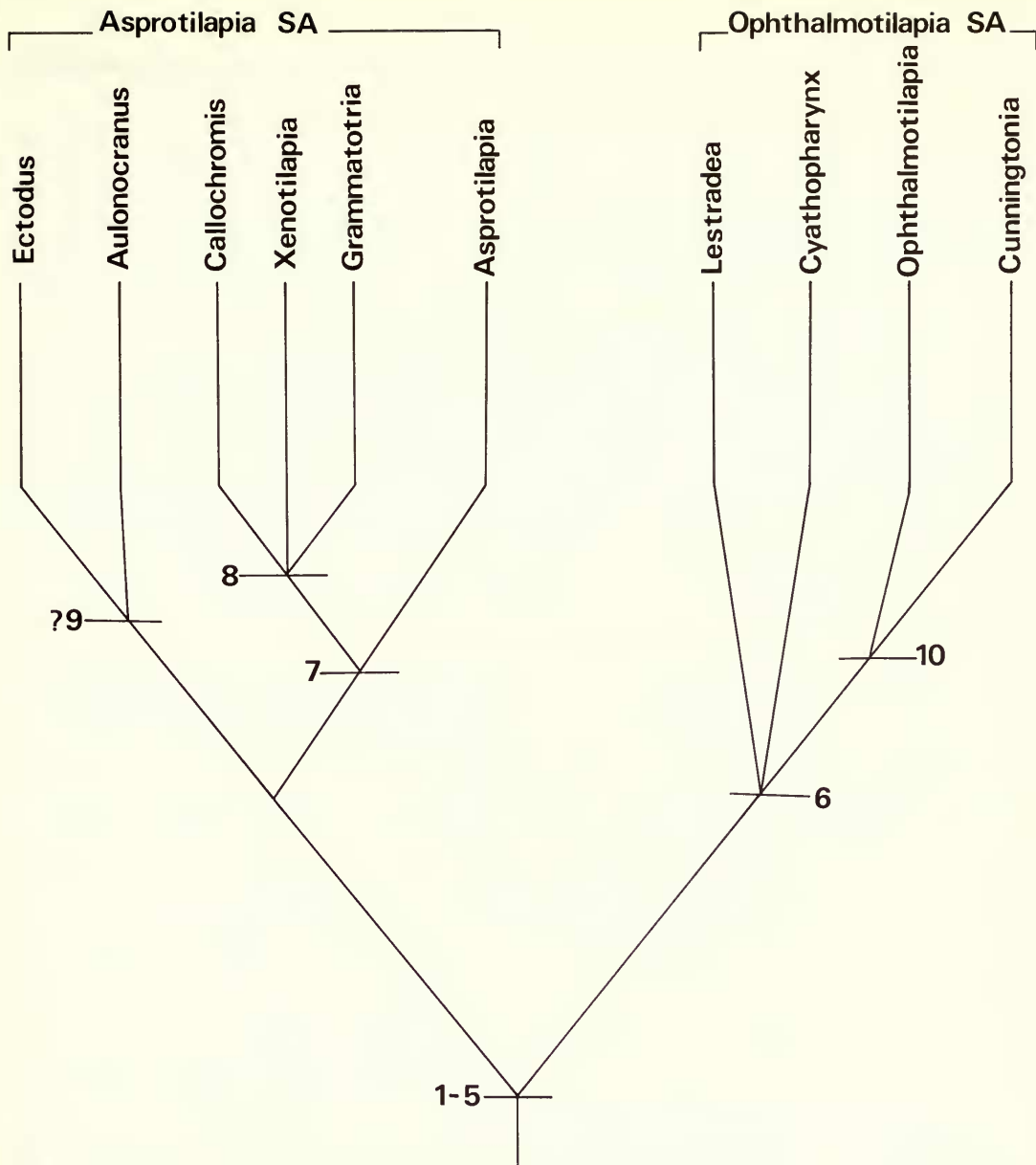
In effect, the main difference between the schemes proposed by Regan (1920) and Fryer & Iles (1972) lies in the latter authors not portraying any taxa in an ancestor-descendent relationship, as was implied, or stated explicitly, in Regan's treatment. Also, Fryer & Iles indicate a more distant relationship than did Regan between *Limnotilapia* (i.e. *Simochromis*) and other members of the latter author's *Ophthalmotilapia* group (see above, p. 275).

In their final analysis Fryer & Iles are less definite in their suggested relationships than was Regan (see figure 337 in Fryer & Iles, 1972 : 507); their phylogram was to be '... regarded as extremely tentative'.

Liem's (1981) wide ranging review of the OA is, in its treatment of anatomical and morphological detail, far more thorough than either of the other two reviews. It was also the first to employ a basically cladistic (*sensu* Hennig, 1966, phylogenetic *sensu* Wiley, 1981) methodology.

Liem brought together certain taxa from Regan's two major groups (see above p. 275), namely *Ectodus* with some elements of Regan's *Ophthalmotilapia-Asprotilapia* group, but excluded other taxa from his *Ectodus-Grammatotria* assemblage (see p. 275 above).

The present analysis (also cladistically based) finally brings together, in a single lineage, all but one pair of taxa from Regan's two groups, the exceptions being *Petrochromis* and the Malawian genus *Petrotilapia* (see above, p. 275). It also includes *Aulonocranus* (but not *Trematocara*) from a third group which Regan implied had some relationship with his *Callochromis-Grammatotria* lineage (Regan, 1920 : 53). Effectively it hypothesizes that the two major Regan groups are sister lineages within a larger taxon which, following Liem (1981), can be named, informally, the *Ophthalmotilapia* assemblage (see Fig. 14).



**Fig. 14** Cladogram for the *Ophthalmotilapia* assemblage based on the 10 apomorphic characters discussed in this paper. Page numbers, given in brackets after each numbered character, refer to those pages on which the character is discussed in detail.

An interrogation mark precedes character 9 since its apomorphic status is doubtful (see p. 272).

- (1) Palatopterygoid gap (p. 254)
- (2) Auricular process on the operculum (p. 259)
- (3) Morphological features of the palatine bone (p. 257)
- (4) Outline shape of the lachrymal (1st infra-orbital bone), and the presence of six laterosensory canal pores (p. 259)
- (5) Adductor fossa on the lateral aspect of the anguloarticular bone (p. 261)
- (6) Intestine long and transversely coiled (p. 264)
- (7) Presence of a pharyngeal hanging pad and associated modifications to the gill-raker morphology (p. 265)
- (8) Dentary with a distinct 'step' (p. 267)
- (9) First branched pelvic fin ray produced (p. 272)
- (10) Dorsal part of the flange behind the vertical part of the preopercular laterosensory canal not narrowing abruptly (p. 273)



## Summary of the taxonomic conclusions and a discussion of the sister-group problem in these and other lake cichlids

The *Ophthalmotilapia* assemblage, originally comprising the genera *Ectodus*, *Lestradea*, *Asprottilapia*, *Cunningtonia* and *Ophthalmotilapia* (Liem, 1981) can now be expanded to include *Xenotilapia*, *Callochromis*, *Grammatotria*, *Aulonocranus* and *Cyathopharynx* (with which is synonymized *Cardiopharynx*).

Taxonomically, the assemblage is recognized as a monophyletic lineage on the grounds of its member species sharing a unique congruence of five apomorphic characters (pages 254–262; Fig. 14).

Two major sublineages can be recognized within the assemblage.

One, characterized by having a short and simple coiled intestine, comprises the genera *Ectodus*, *Aulonocranus*, *Asprottilapia*, *Xenochromis*, *Callochromis* and *Grammatotria*. It can be further subdivided on the basis of various synapomorphies shared by four of its members (see pages 263–274 and Fig. 14).

The other major sublineage contains *Lestradea*, *Ophthalmotilapia*, *Cunningtonia* and *Cyathopharynx*, species in which the intestine is long and complexly coiled (see pages 264–265). Attempts to subdivide this lineage have not proved satisfactory, but it would seem that *Lestradea* is the plesiomorph sister-group of the other three genera (pages 271–274 and Fig. 14); possibly amongst these three genera *Ophthalmotilapia* and *Cunningtonia* are sister taxa, but the entire group is, for the moment, probably best treated as an unresolved polychotomy.

No sister-group, or even a single taxon, has so far been satisfactorily identified amongst the cichlids of Lake Tanganyika. Regan's (1920 : 52) suggestion of close relationship between *Limnotilapia* (i.e. *Simochromis*, see Greenwood, 1979) and *Ophthalmotilapia* (and hence *Cyathopharynx*, *Asprottilapia* and *Cunningtonia* as well) cannot be corroborated on the basis of shared synapomorphies.

When comparisons are made with other Tanganyika taxa the results are equally unproductive except that two OA group synapomorphies occur, singly, in some species of '*Limnochromis*' and *Trematocara*.

For example, in *Trematocara marginata*, but in no other species, there is a poorly differentiated OA-like projection from the anteroventral angle of the lachrymal (see p. 259). A similar projection occurs in '*Limnochromis*' *permaxillaris* and '*L.*' *pfefferi*, both of which are now placed in Poll's genus *Gnathochromis*. Both the '*Limnochromis*' species and *Trematocara marginata* have only 5 pores in the lachrymal, but other '*Limnochromis*' species which lack the projection, '*L.*' *otostigma*, *L. auritus* and *L. abeei*, have 5 or 6 pores.

Neither *Trematocara* nor '*Limnochromis*' has the characteristically shaped lachrymal of the OA species, and the distribution pattern of the two OA group-features indicates an independent (i.e. homoplastic) origin in the two genera.

Regan's (1920 : 53) suggested relationship between *Aulonocranus* and *Trematocara* apparently stems from the hypertrophied laterosensory canals, and pores, present in both taxa. Apart from that feature, and the weak OA-type lachrymal peak in one species of *Trematocara*, there are no derived features uniquely shared by the two genera. Admittedly there is a trend amongst the OA species for there to be some degree of hypertrophy in the laterosensory canal system of the lachrymal. But, in the absence of other synapomorphies it would be unrealistic to use a trend character as a basis for suggesting group relationships, especially when that trend occurs in several other lineages as well. In this particular instance, too, the lowest degree of canal enlargement is found in those OA species with the least number of derived features (i.e. *Ectodus* and *Lestradea*), and which are therefore taken to be the plesiomorph members of their respective subassemblages.

The tentative phylogenetic schemes proposed by Fryer & Iles (1972 : 507, fig. 337) are not always arranged so as to suggest sister-group relationships with taxa outside the OA. They do, however, show *Leptochromis* (i.e. *Reganochromis*) as a sister taxon of *Ectodus*, *Callochromis*, *Xenotilapia* and *Grammatotria*, and *Aulonocranus* is paired with

*Trematocara*. Once again, there are no shared derived features to substantiate such relationships, and none which might indicate that either *Reganochromis* or *Trematocara* is the sister-group, or part of the sister-group, to the *Ophthalmotilapia* assemblage.

The only taxon which consistently shows more than a single *OA* group synapomorphy amongst a number of its species is the Malawian genus *Lethrinops*.

I have examined alizarin preparations and dry skeletons of five *Lethrinops* species, the type species *Lethrinops lethrinus*, and *L. praeorbitalis*, *L. parvidens*, *L. auritus* and *L. longimanus*. In all there is a distinct palatopterygoid gap and a well-defined, although not extensive *OA* type adductor fossa on the anguloarticular bone (Figs 15 & 16).

The palatopterygoid gap is relatively smaller than in most *OA* species, but in none of the *Lethrinops* species examined is there any contact between the palatine and the entopterygoid. Unlike members of the *OA*, the *Lethrinops* species have a much deeper entopterygoid, and one that either rests along the upper margin of the quadrate or slightly overlaps that bone medially. In *OA* species, most of the entopterygoid lies medial to the quadrate, and is thus largely obscured by it in lateral view. As a consequence of this spatial relationship the dorsal margin of the entopterygoid in *Lethrinops* lies at a level nearer the palatine head than it does in *OA* species.

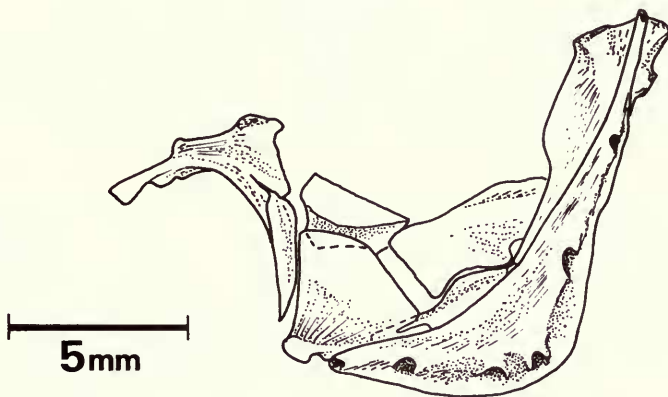


Fig. 15 Left suspensorium of *Lethrinops lethrinus*.

The shape of the palatine (Fig. 15) in *Lethrinops* differs somewhat from that in the *OA* taxa (see p. 257 above). Its posterior margin is slightly concave, and the angle between this margin and the head of the bone is less nearly rectangular; the posterodorsal margin contributing to the angle is also less acute in *Lethrinops*; indeed, in some specimens and species it is almost rounded. But, as in the *OA* species the body of the bone is expanded posteriorly so that the bone's proportions are nearer those of the *OA* type than that commonly found amongst African cichlids.

The occurrence of this particular palatine shape in association with a palatopterygoid gap raises the question of whether or not the two characters are correlated. That a similarly shaped palatine does occur in at least two species without a palatopterygoid gap (viz. *Limnochromis abeei* [Lake Tanganyika] and *Astatotilapia macropoides* [Lakes Edward and George]), would seem to argue against correlation, but the possibility requires further testing.

The adductor fossa in *Lethrinops* (Fig. 16) is well defined but, as compared with the fossa in members of the *Asprotilapia* subassemblage amongst the *OA* (p. 261) it is less extensive. It is, however, comparable with the fossa in members of the *Ophthalmotilapia* subassemblage (p. 265).

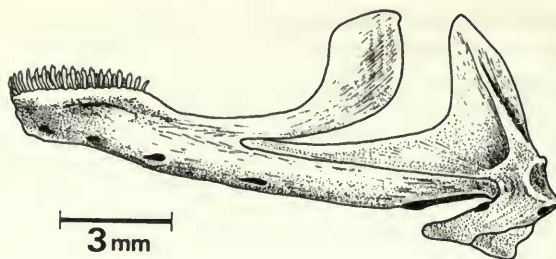


Fig. 16 Left dentary and anguloarticular of *Lethrinops lethrinus*, lateral view.

An adductor fossa of this type is not restricted to members of the *OA*, but also occurs in several seemingly unrelated taxa, including some '*Haplochromis*' species from Malawi (see p. 261). Thus, in itself, the fossa cannot be considered a unique apomorphy; its value as a group synapomorphy stems solely from its congruence with other apomorphic characters.

There is a third derived character found in the five *Lethrinops* species which is also present in one subgroup of the *OA*, namely a stepped dorsal margin to the dentary, with the teeth confined to the higher level of the step (Fig. 16). Amongst the *OA* taxa this feature is found only in *Xenotilapia*, *Callochromis* and *Grammatotria* (all members of the *Asprotilapia* subassemblage; see p. 267). Its restricted distribution within the *OA* considerably reduces its potential significance as a character indicative of a possible relationship between *Lethrinops* and the *OA*. That it apparently occurs only in these *OA* species and in *Lethrinops*, and that both groups have a palatopterygoid gap is, nevertheless, intriguing and requires further investigation.

Attempts to evaluate the two apomorphic features shared by *Lethrinops* and the *OA* in its entirety (i.e. the palatopterygoid gap and the adductor fossa) are hampered by lack of comparative data from the Malawi cichlids as a whole. A relatively superficial survey shows, however, that the adductor fossa is present only in some haplochromine species (see p. 261). Whether or not these haplochromines are closely related to *Lethrinops* has not been adequately tested, but preliminary investigations do not suggest that this is the case.

The situation regarding the palatopterygoid gap is different. I have examined specimens of all the described genera of Malawi fishes, but by no means all their included species. In none is there a palatopterygoid gap. Thus, the character appears restricted to *Lethrinops* and the *OA* (see also p. 255).

In summary, it seems that no group of Lake Tanganyika cichlids consistently shows one or more of the group synapomorphies for the *OA*. On the other hand, in Lake Malawi at least some species of *Lethrinops* share two derived features with all members of the *OA*, and only one of these features (the adductor fossa) occurs in other Malawi taxa. The *Lethrinops* species also have a third derived feature, the shape of the dentary, which is present in one lineage amongst the *OA*.

As it stands, this indication of a possible sister-group relationship between the *OA* and *Lethrinops* is no more than suggestive. It could well be refuted as an example of convergence when more is known about the interrelationships of the cichlids from Lake Malawi and those of Lake Tanganyika.

There are several cases of close similarity existing between certain features in endemic taxa of each lake, but few between species in those lakes and endemic taxa from Lake Victoria.

As examples one may mention that the dentition in *Cunningtonia* is virtually identical with that in *Petrotilapia* and there are marked similarities in the jaw anatomy of the two genera (*Petrochromis* from Lake Tanganyika can also be included in this example); or, the morphology of the dentary in *Asprotilapia* which is like that of *Labeotropheus* a Malawian genus also sharing several features with *Tropheus* from Lake Tanganyika. Finally, one can cite the many similarities in syncranial architecture existing between *Simochromis* of Tanganyika and the *Pseudotropheus* species complex of Lake Malawi.



These are by no means the only cases that can be, or have been, cited of supposed convergence or parallelism between the cichlid faunas of the two lakes (see Fryer & Iles, 1972). Adequate explanations for these similarities are, however, far more difficult to find.

An example of similarity involving much greater geographical separation than that between Tanganyika and Malawi, and one which incorporates a greater number of species as well as a mosaic distribution of similar characters amongst the species, involves two members of the *OA*, another, unrelated, genus from Lake Tanganyika, a Malawian taxon and *Neopharynx schwetzi*, a monotypic genus from the lower Fwa (Kasai drainage in south-western Zaire; for a full description of *N. schwetzi*, see Poll, 1948).

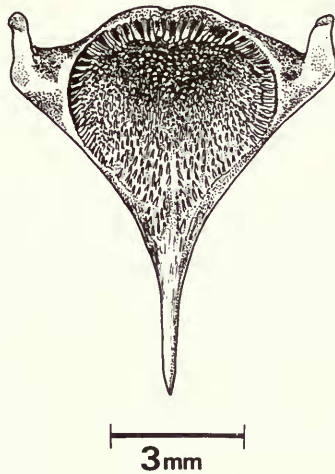


Fig. 17 Lower pharyngeal bone of *Neopharynx schwetzi*, occlusal view (from a specimen in paratypical series, MRAC 71291–71299).

*Neopharynx schwetzi* has a lower pharyngeal bone morphologically and dentally almost identical with that of *Cyathopharynx* (see Figs 17 & 24). Its oral dentition, in contrast, is virtually identical with that in *Petrochromis* (Tanganyika) and *Petrotilapia* (Malawi), and is quite unlike that in *Cyathopharynx*. As far as the morphology of the teeth is concerned, but not their distribution on the dentary, *Neopharynx* also closely resembles *Cunningtonia* of Lake Tanganyika. It differs from all three taxa in the shape of its premaxilla, but the morphology of the premaxillary teeth is, as might be expected, very similar in all four genera.

The relationships of *Neopharynx* have yet to be established; probably they lie with two other Fwa endemics, *Cyclopharynx* and *Callopharynx*, genera having an extreme development of the *Neopharynx*-*Cyathopharynx* type of lower pharyngeal bone (for details see Poll, 1948).

*Neopharynx* has neither an *OA* type lachrymal, a palatopterygoid gap, nor an *OA*-type of adductor fossa, and the shape of its palatine bone is close to the generalized form. Thus the similarities between *Neopharynx*, *Cyathopharynx* and *Cunningtonia* are undoubtedly homoplastic, as most probably are the similarities shared with *Petrochromis* and *Petrotilapia*.

The *Neopharynx* example underlines the problems involved in attempting to work out interrelationships amongst cichlid fishes, as do the repeated appearances of certain derived features shown by members of the *Ophthalmotilapia* assemblage in species which appear to be but distantly related to the *OA*.

Surmises about the interrelationships of African lake cichlids have, I believe, been unduly influenced, perhaps even inhibited, by three major factors. Firstly, the idea that there are two

basic lineages, a '*Tilapia*' line and a '*Haplochromis*' one (see discussion in Greenwood, 1978; also p. 274 above). Secondly, that the major lakes are, faunistically, closed basins and have been so almost since their inception, with the result that the cichlids of a lake are presumed to have evolved from one or a few ancestral species originally trapped there (see discussion in Fryer & Iles, 1972; and Greenwood, 1974). In other words, assumed histories for the lakes have been given too great a weight in deciding whether a feature was the result of convergence, parallelism, or the consequence of common ancestry.

The third, and overriding, factor is a paucity of specific and critical studies on the phylogeny of the fishes. Overall resemblances, or the use of characters without adequate outgroup comparisons, are often major weaknesses influencing decisions on relationships.

The effect of these three factors has resulted in a tendency to restrict the search for sister-groups to a single lake and to the appropriate '*Tilapia*' or '*Haplochromis*' lineage. Admittedly, at lower levels of universality sister species are generally to be found within the same lake or proto-lake system (Greenwood, 1980); the problems arise when attempting to establish relationships at somewhat higher taxonomic levels. The *Ophthalmotilapia* assemblage, and the search for its sister-group are good examples of problems encountered at these two levels.

The existence of endemic species flocks, the superficially close similarity of species in different flocks, and indeed of many different taxa outside the lakes, all help to complicate the issue. Under such circumstances the possibility and probability of homoplasy are theoretically enhanced, as in practice are the problems associated with their resolution.

What is needed to resolve these problems are tests of the assumption that a so-called species flock is really of monophyletic origin. If a lake's cichlid fauna was derived from a few species which are not true sister species, and if the true sister taxa were the ancestors of another flock, then the situation suggested by the apparent relationship of *Lethrinops* (Malawi) and the OA (Tanganyika) could well be a real one. The idea first put forward by Regan (1922) that the Malawi 'flock' carries indicators of its monophyly must be seriously questioned (Greenwood, in press). No indicators of monophyly have been suggested for the Tanganyika 'flock' (even at the levels of the supposed '*Tilapia*' and '*Haplochromis*' type basic stocks). The possibility of a close relationship between the faunas of the two lakes deserves very careful examination.

### The status of *Cyathopharynx* Regan, 1920 and *Cardiopharynx* Poll, 1942

In his original description of the monotypic genus *Cardiopharynx*, Poll (1942 : 346) noted the great similarity between its peculiarly shaped lower pharyngeal bone and the lower pharyngeal of *Cyathopharynx*. He differentiated the two genera because *Cardiopharynx* has, as compared with *Cyathopharynx*:

- (i) Larger scales (36–38 cf 48–64 in a longitudinal series (see Poll, 1956 : 127).
- (ii) Jaw teeth in two rows, the teeth, in both jaws, of equal size (cf 3–5 rows; teeth in the outer row larger than those of the inner rows).
- (iii) Dentigerous surface of the lower pharyngeal bone cardiform (cf rounded in *Cyathopharynx*)
- (iv) Supraoccipital extending forward to a level above the anterior margin of the orbit (cf to the mid-orbital region only)
- (v) Parietal crests ending above the centre of the orbit (cf extending to a point above the posterior part of the orbit)
- (vi) More vertebrae (36, i.e. 17 + 19) cf 32–34 (i.e. 16 or 17 + 16 or 17)

Poll gives no reasons why these characters should be used to separate the taxa at a generic level, and neither does he indicate why the great similarity in pharyngeal morphology, and its uniqueness, should be outweighed as an indicator of close phyletic relationship by the diagnostic characters he enumerates.

None of these latter features can be considered uniquely apomorphic for *Cardiopharynx*, and now that more material is available several are found to be less trenchant than was first thought to be the case, as the following comments show.

The teeth in both jaws of all *Cardiopharynx* specimens I examined are invariably arranged in two rows, but in *Cyathopharynx* there is a greater variation than was intimated by Poll (1942 & 1956). In the majority of specimens examined, the inner premaxillary row is, in places, irregularly arranged so as to give the appearance of a double row wherever the irregularities occur. Occasionally there are specimens in which the inner tooth row is clearly and regularly double, thus giving a total count of three tooth rows; also occasionally it is distinctly single, giving a total of two rows. In none of the specimens is there a total of more than three premaxillary rows. The inner row of teeth in the dentary is generally single; in a few fishes, however, it is somewhat irregular and so comes to resemble the modal condition in the premaxilla.

Contrary to Poll (1946), I can find no marked difference between the taxa in the relative size of inner and outer teeth. In both genera the outer teeth, in both jaws, are clearly taller and stouter than those of the inner row or rows, and not of equal size in *Cardiopharynx* as claimed by Poll. The most that can be said is that in *Cardiopharynx* the size difference between outer and inner row teeth is a little less marked than in *Cyathopharynx*.

In a later redescription of both taxa, Poll (1956) commented on the outer teeth of *Cardiopharynx* being more or less tricuspid in young fishes, but he gave no size-range over which tricuspid teeth are found. In specimens 60–105 mm SL I have examined, there are no outer tricuspid teeth, whereas in specimens of *Cyathopharynx* of a comparable size range and up to 112 mm SL, distinctly, and also weakly, tricuspid teeth do occur. In larger *Cyathopharynx* specimens the teeth are exclusively and clearly unicuspid.

The difference in the shape of the dentigerous surface of the lower pharyngeal bone (iii above, p. 282) is due entirely to a marked median depression in the posterior face of the bone and of the toothed area in *Cardiopharynx*. In *Cyathopharynx* this margin of the bone is slightly and more broadly indented, and there is no indentation of the posterior tooth row (Fig. 23).

In all other respects the lower pharyngeal bone in both taxa is identical. As noted above (p. 271) it represents a uniquely derived condition amongst the cichlids of Lake Tanganyika.

The shape of the pharyngeal teeth, tall and slender, with spatulate crowns that are not broader than the neck, and their cardiform pattern on the alveolar surface of the bone, is the same in both genera (Fig. 24). Likewise, the morphology of the principal upper pharyngeal bones is identical, as is the morphology and pattern of their teeth. Unlike the lower teeth, those on the upper pharyngeal bones do have a slight, shoulder-like cusp at the base of the spatulate crown surface.

The anterior point reached by the supraoccipital and parietal crests (iv & v above) is variable intragenerically. In the skulls I have examined there are specimens from each genus showing conditions intermediate between those originally used as diagnostic features for the two genera.

Finally, there are the supposedly intergeneric differences in vertebral number (vi above). I have examined 15 specimens of *Cardiopharynx schoutedeni* (13 from radiographs, 2 as alizarin preparations), and 12 of *Cyathopharynx furcifer* (10 from radiographs and 2 dry skeletons), and obtained the following counts:

*Cardiopharynx*: Total number (excluding the fused  $U_1$ – $PU_1$  centra) 33 (f5) and 34 (f10), comprising 15 (f1), 16 (f7) or 17 (f7) abdominal and 16 (f1), 17 (f9) or 18 (f5) caudal elements.

*Cyathopharynx*: Total number (excluding the fused  $U_1$ – $PU_1$  centra) 32 (f5) 33 (f6) or 34 (f1), comprising 16 (f9) or 17 (f3) abdominal and 16 (f7) or 17 (f5) caudal elements.

The differences in range are not very marked and there is a complete overlap in other counts, but with a slight difference in the modal number for total [34 cf 33] and abdominal counts [17 cf 16] for *Cardiopharynx* and *Cyathopharynx* respectively.

Thus, of Poll's (1942) original diagnostic features, only the difference in scale size remains.



There are, however, other differences which were noted in the original diagnosis. *Cyathopharynx* has proportionately longer pelvic fins, in males the tip of this fin reaches the last anal fin ray or even to as far as the caudal fin fork; in *Cardiopharynx* it reaches only to about the middle of the anal fin. Also, in *Cyathopharynx* the first pelvic ray is clearly the longest whereas in *Cardiopharynx* either the first and second rays are equally protracted or the second ray may be the longest.

Other differences involve neurocranial shape (Figs 18 & 19). *Cardiopharynx* has a shallower skull than does *Cyathopharynx*, the prootic portion of its otic bulla is more inflated, and the interorbital region is much narrower.

Undoubtedly the two taxa are distinguishable. The problem is to decide at what taxonomic level their separation should be recognized.

To recognize two genera on the basis of the differences discussed above is to obscure the fact that, amongst the Lake Tanganyika cichlids, *Cyathopharynx* and *Cardiopharynx* share a unique apomorphy (the form of the lower pharyngeal bone) which would indicate a common ancestry not shared with any other taxon. That relationship is, I believe, best indicated by treating the two species as members of a single genus, *Cyathopharynx* Regan, 1920.

### *Cyathopharynx* Regan, 1920

*Cyathopharynx* Regan, 1920. *Ann. Mag. nat. Hist.* (9), 5: 42–43.

*Cardiopharynx* Poll, 1942. *Revue Zool. Bot. afr.*, 36: 346–347.

TYPE SPECIES. *Tilapia grandoculis* Boulenger, 1899. *Trans. zool. Soc. Lond.* 15: 94, pl. XIX, fig. 6.

Poll (1946 : 283–4) has synonymized this species with *C. furcifer* (Blgr), 1898.

DIAGNOSIS. A member of the *Ophthalmotilapia* assemblage, distinguished from other members of that group by having a cardiform dentigerous surface to the lower pharyngeal bone, the body of which is inflated and nearly cardiform in outline.

*Cyathopharynx* is distinguished from other species with a cardiform alveolar surface to the lower pharyngeal bone by, among other features, its OA group characters (see p. 262) and by the marked elongation of the first, or first and second pelvic fin rays in adult male fishes; these protracted rays extend to at least the middle of the anal fin, and in one species, sometimes as far as the fork of the caudal fin.

### Description

*Neurocranium* (Figs 18 & 19). In its general outline, the skull differs little from that of the generalized haplochromine type in which the preorbital profile is slightly decurved. The orbit, however, is relatively larger than in a generalized skull, and the otico-occipital region is shorter, a correlate, probably, of the enlarged orbit since the ethmoid region retains the same proportions as in a generalized skull.

The ventral apophysis for the upper pharyngeal bones is of a weak '*Tropheus*' type, in which the basioccipital barely contributes to the articular surface (see Greenwood, 1978; also p. 274 above).

*Suspensorium* (Figs 1C & D). As in other members of the *Ophthalmotilapia* assemblage, there is a distinct palatopterygoid gap (see p. 255), and the entopterygoid is shallow, with only one-third to one-quarter of its depth visible above the quadrate margin. The hyomandibula has a narrow flange anterior and dorsal to the symplectic process. The shape and proportions of the symplectic are typically those of an OA species (see p. 256).

*Infraorbital series* (Figs 3A & F). The lachrymal bone (1st infraorbital) has the typical outline shape, and the anteroventral process, of an OA taxon (see p. 259). There are six pores opening from the laterosensory canal system, the tubular part of which is somewhat

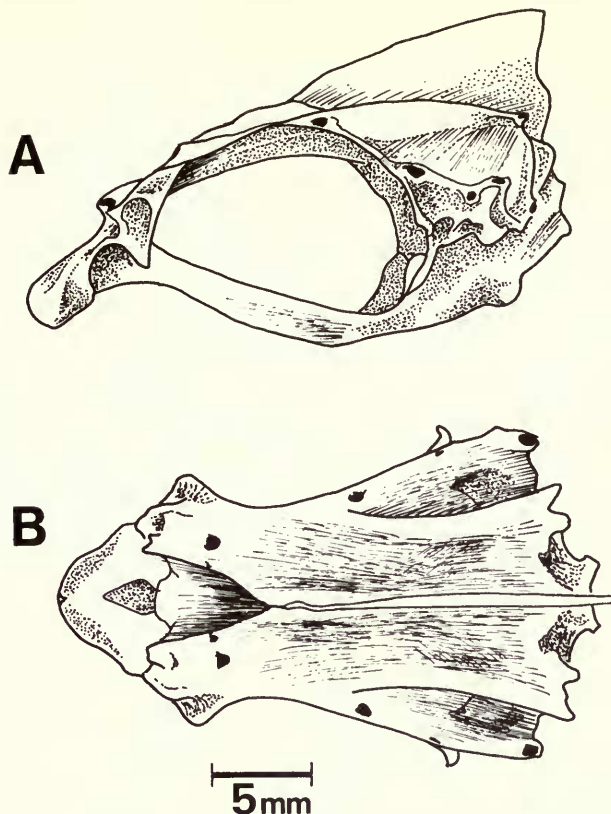


Fig. 18 Neurocranium of *Cyathopharynx furcifer* in : A, left lateral view; B, dorsal view.

inflated. The pores, however, do not show a corresponding enlargement (i.e. they do not deviate noticeably from the generalized condition). The other infraorbital bones are little more than tubular ossifications around the sensory canal, but do have low dorsal and ventral keels.

**Myology.** Division I of the *adductor mandibulae* complex has an extensive origin along the vertical limb of the preoperculum, but division II has its preopercular origin mainly from the horizontal limb of that bone; only a small area extends onto the vertical limb.

The dorsal gill-arch muscles compare closely, in most respects, with those of other OA species (see Liem, 1981 : 196–7 & 205, & fig. 8; also p. 258 above). The *retractor dorsalis* muscles are especially well developed with, in some individuals of both species, indications of a subdivision into dorsal and ventral components.

**Dentition** (Fig. 20). Some aspects of the oral dentition have been commented upon already (p. 283 above). The outer row teeth in both jaws are tall and slender. In *C. furcifer* the crown is slightly broader than the neck and shaft of the tooth, whereas in *C. schoutedeni* the crown is no wider than the shaft. The crowns are slightly recurved in both species.

Premaxillary outer row teeth are aligned vertically to the alveolar surface, but in the dentary the teeth situated anteriorly and anterolaterally are procumbent. The posterior dentary teeth are vertical, those of *C. furcifer* continuing for some distance up the coronoid process.

Inner row teeth in both jaws, and both species, are noticeably smaller than those of the outer row, and are implanted so as to lie almost horizontally.

**Mouth.** The lips are thin, and the gape is horizontal.

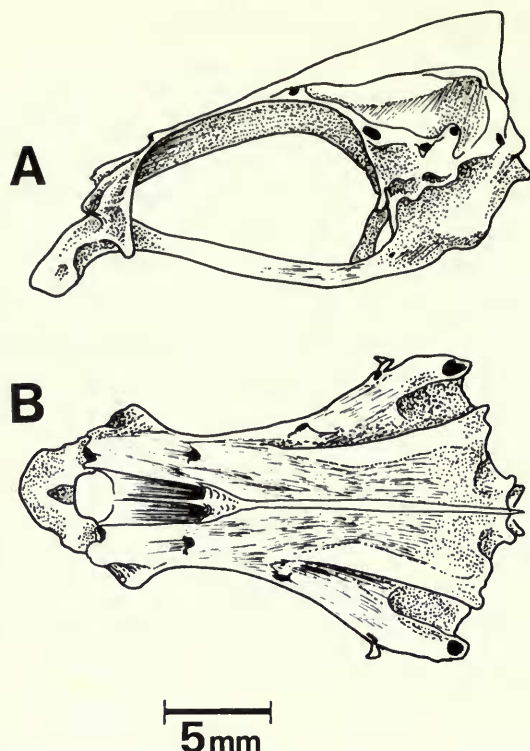


Fig. 19 Neurocranium of *Cyathopharynx schoutedeni* in : A, left lateral view; B, dorsal view.

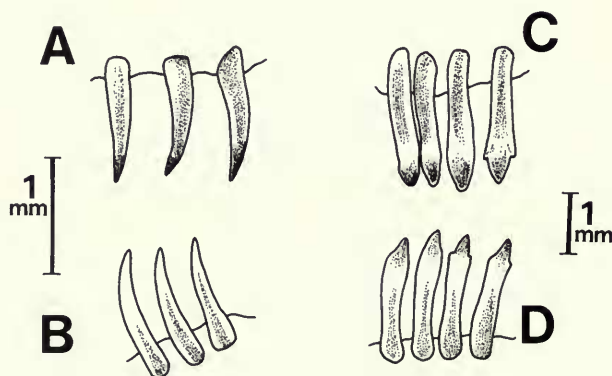


Fig. 20 Outer row jaw teeth (drawn *in situ*) from : A & B, *Cyathopharynx schoutedeni*, specimen 103 mm SL (premaxillae and dentary respectively); C & D, *C. furcifer*, specimen 113 mm SL (premaxilla and dentary, respectively). Dentary teeth viewed from below.

*Jaws.* The dentary in both species is a moderately slender bone, shallower and less robust in *C. schoutedeni* than in *C. furcifer* (Fig. 21). Anteriorly and anterolaterally the dorsal aspect of the bone is expanded into a broad surface which extends outwards to overhang, as a narrow shelf, the body of the bone. The tooth rows occupy only the outermost part of the surface, with the result that there is a wide expanse of bone lying medial to them. The laterosensory canal system and its openings in *C. furcifer* are more cavernous than those in *C. schoutedeni*.

The anguloarticular has a well-defined but short fossa for the *adductor mandibulae* muscle, with the ridge delimiting its anterior margin particularly deep and prominent. The premaxilla (Fig. 22) has no especially outstanding features.



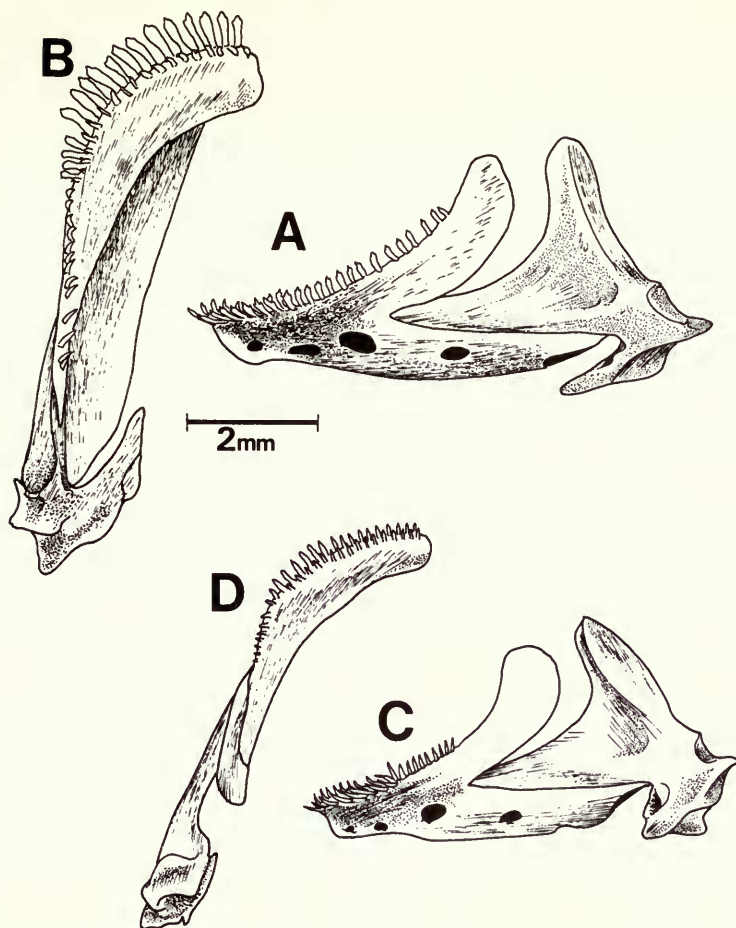


Fig. 21 Dentary and anguloarticular, in left lateral and occlusal views respectively, of: A & B, *Cyathopharynx furcifer*; C & D, *C. schoutedeni*.

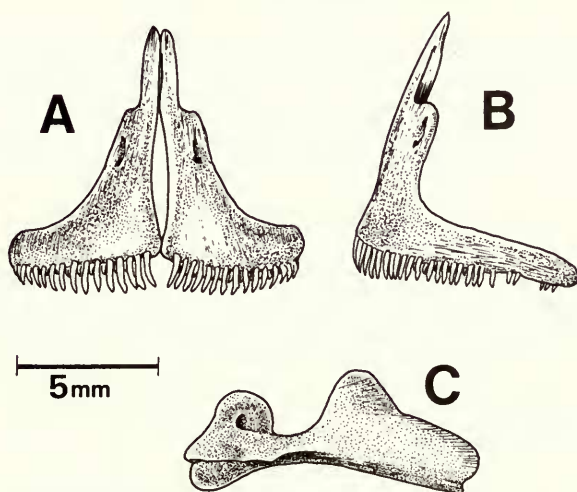


Fig. 22 A & B, premaxilla of *Cyathopharynx furcifer*, anterior and lateral view; C, maxilla (left) seen from a slightly ventrolateral viewpoint.

As compared with the generalized type of maxilla, that in *Cyathopharynx* is foreshortened and has a well-developed, long-based posterior process (see also p. 269).

*The pharyngeal bones.* The shape and other peculiar features of the lower pharyngeal bone (Fig. 23) are described on page 283.

The upper pharyngeal bones differ less markedly from the usual condition seen in African cichlids. The outline of the alveolar surface of the major element (pharyngobranchial 3) is noticeably ovoid, but otherwise differs little from the generalised condition. Their principal difference lies in the relatively greater alveolar surface area, and its more elongate proportions. Other differences are found in the less prominent facets for articulation with the 3rd and 4th epibranchials, and in the lower summit facet (nomenclature following Barel *et al.*, 1976 : 214, fig. 26).

The lower pharyngeal teeth (Fig. 24) are slender, near cylindrical in cross-section and are closely packed. Those at the periphery of the dentigerous area are weakly curved, the others

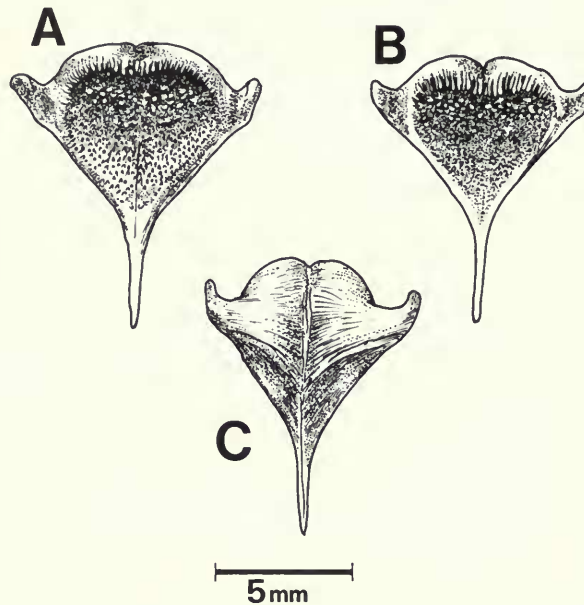


Fig. 23 Lower pharyngeal bone, in occlusal view of: A, *Cyathopharynx furcifer*; B, *C. schoutedeni*, and, in ventral view, C, of *C. furcifer*.

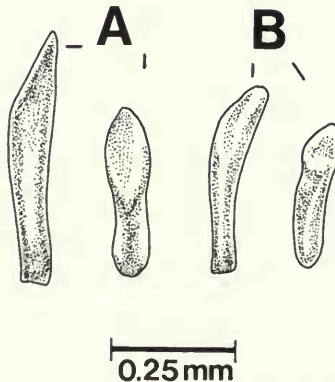


Fig. 24 *Cyathopharynx furcifer*, pharyngeal teeth (lateral and semioclusal views) from : A, the posterior; and B, anterior dental fields.

erect. There is a noticeable and rapid increase in the height of the teeth forming the posterior 5 or 6 rows, with the teeth of the posterior row tallest and stoutest. The elongate crown of each tooth is flat, and slopes gently upwards and backwards. There is no indication of a low shoulder-like projection or cusp at the base of the crown.

The shape and dense arrangement of the upper pharyngeal teeth are very similar to those of the lower bone, the teeth differing only in having a small shoulder or cusp at the base of the posteriorly directed crown.

*Vertebrae.* Regan (1920 : 43), in his original description of *Cyathopharynx*, noted that the third vertebra lacks an inferior apophysis, from which the *retractor dorsalis* muscles originate. In four of the five dry skeletons and alizarin preparations I examined, a low apophysis is present on the fourth centrum in one fish and on the fifth centrum in three others, but none is present in the fifth specimen.

Vertebral counts for the two species are given on page 283.

*Squamation.* Scales on the body are weakly ctenoid except for the cycloid scales on the chest and belly. Those covering the thoracic region are small, and are fairly abruptly demarcated from the larger scales on the ventral flanks and the belly.

The two *Cyathopharynx* species differ, disjunctly, in the size of their body scales, with *C. schoutedeni* having 36–38 scales in a longitudinal series, and *C. furcifer* 48–64. The species also differ, slightly, in the posterior extension of the upper lateral line pore scales, those in *C. furcifer* usually extending almost to the caudal fin base, whereas in *C. schoutedeni* the pore scales terminate at a level 3 or 4 scale rows anterior to the caudal base. There is, however, some interspecific overlap in this feature.

*Fins.* Little can be added to the description (p. 272) of the protracted first or first and second pelvic fin rays in adult males. In females and juvenile males these rays are also noticeably longer than the others, but usually do not extend beyond the level of the anus; exceptionally they may reach the spinous part of that fin.

The caudal fin is forked; adult males have the two upper- and lowermost principal branched rays produced into fine filaments. Rows of small, barely overlapping scales are present on the fin membrane (except between the three middle rays), and extend to the level of the fork.

*Gut.* The intestine is long (*ca* 3 to 4 times SL) and complexly coiled in a predominantly transverse direction (see p. 264).

### Contained species

*Cyathopharynx furcifer* (Blgr) 1898

*Cyathopharynx schoutedeni* (Poll) 1942

Both are lacustrine species endemic to Lake Tanganyika; for detailed descriptions, figures and biological data see Poll (1956 : 130–137 & 125–130 for the species respectively).

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## References

- Barel, C. D. N., Witte, F. & van Oijen, M. J. P. 1976. The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **26** (2): 163–265.
- Boulenger, G. A. 1898. Report on the collection of fishes made by Mr J. E. S. Moore in Lake Tanganyika during his expedition, 1895–96. *Trans. zool. Soc. Lond.* **15** (1): 1–30.
- Brichard, P. 1978. *Fishes of Lake Tanganyika*. T.F.H. Publications Inc., New Jersey & London.
- Fryer, G. & Iles, T. D. 1972. *The cichlid fishes of the Great Lakes of Africa. Their biology and evolution*. Oliver & Boyd, Edinburgh.
- Greenwood, P. H. 1965. Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis aluauudi* and their taxonomic implications. *Proc. Linn. Soc. Lond.* **176**: 1–10.
- 1974. Cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. Br. Mus. nat. Hist. (Zool.)* Suppl. 6: 1–134.
- 1978. A review of the pharyngeal apophysis and its significance in the classification of African cichlid fishes. *Bull. Br. Mus. nat. Hist. (Zool.)* **33**: 297–323.
- 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. *Bull. Br. Mus. nat. Hist. (Zool.)* **35**: 265–322.
- 1980. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II: the species from Lakes Victoria, Nabugabo, Edward, George and Kivu. *Bull. Br. Mus. nat. Hist. (Zool.)* **39**: 1–101.
- 1981. *The haplochromine fishes of the East African Lakes*. Kraus-Thomson Organization GmbH, Munich & London.
- Hennig, W. 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana.
- Liem, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Zool.* **22** (4): 425–441.
- 1981. A phyletic study of the Lake Tanganyika cichlid genera *Asprotilapia*, *Ectodus*, *Lestradea*, *Cunningtonia*, *Ophthalmochromis*, and *Ophthalmotilapia*. *Bull. Mus. comp. Zool. Harv.* **149** (3): 191–214.
- & Osse, J. W. M. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. *Am. Zool.* **15** (2): 427–454.
- & Stewart, D. J. 1976. Evolution of the scale-eating cichlid fishes of Lake Tanganyika: a generic revision with a description of a new species. *Bull. Mus. comp. Zool. Harv.* **147** (7): 319–350.
- Poll, M. 1942. Cichlidae nouveaux du Lac Tanganyika appartenant aux collections du Musée du Congo. *Revue Zool. Bot. afr.* **36** (4): 343–360.
- 1946. Révision de la faune ichthyologique du lac Tanganyika. *Annls. Mus. Congo belge C. Zool. Sér. I*, **4** (3): 141–364.
- 1948. Descriptions de Cichlidae nouveaux recueillis par le Dr. J. Schwetz dans la rivière Fwa (Congo belge). *Revue Zool. Bot. afr.* **41**: 91–104.
- 1956. Poissons Cichlidae. *Résult. scient. Explor. hydrobiol. lac Tanganyika* (1946–1947), 3 fasc. 5b: 1–619.
- 1981. Contribution a la faune ichthyologique du lac Tanganyika. Révision du genre *Limnochromis* Regan 1920. Description de trois genres nouveaux et d'une espèce nouvelle: *Cyprichromis brienii*. *Annals Soc. r. zool. Belg.* **111**: 163–179.
- Regan, C. T. 1920. The classification of the fishes of the family Cichlidae—I. The Tanganyika genera. *Ann. Mag. nat. Hist.* (9) **5**: 33–53.
- 1922. The cichlid fishes of Lake Nyassa. *Proc. zool. Soc. Lond.* **1921**: 675–727.
- Stiassny, M. L. J. 1981. Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika. *Bull. Br. Mus. nat. Hist. (Zool.)* **40**: 67–101.
- Trewavas, E. 1973. On the cichlid fishes of the genus *Pelmatochromis* with a proposal of a new genus for *P. congicus*; on the relationship between *Pelmatochromis* and *Tilapia* and the recognition of *Sarotherodon* as a distinct genus. *Bull. Br. Mus. nat. Hist. (Zool.)* **25**: 1–26.
- 1974. The freshwater fishes of rivers Mungo and Meme and Lakes Kotto, Mboandong and Soden, West Cameroon. *Bull. Br. Mus. nat. Hist. (Zool.)* **26**: 299–419.
- Whitley, G. P. 1928. Studies in ichthyology. No. 3. *Rec. Aust. Mus.* **17**: 101–143.
- Wiley, E. O. 1981. *Phylogenetics*. John Wiley & Sons, New York.